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REPTILE AND AMPHIBIAN TRACKWAYS FROM THE LOWER TRIASSIC MOENKOPI FORMATION OF ARIZONA AND UTAH

BY

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CONTENTS

REPTILE AND AMPHIBIAN TRACKWAYS FROM THE LOWER TRIASSIC MOENKOPI FORMATION OF ARIZONA AND UTAH

BY

FRANK E. PEABODY

(Contribution from the University of California Museum of Paleontology)

INTRODUCTION

In the years 1938 to 1946, summer field parties conducted by the Museum of Paleontology of the University of California have prospected intensively in the Lower Triassic Moenkopi formation in the valley of the Little Colorado River between Cameron and Holbrook, Arizona, and in northern and southern Utah. As a member of the 1938, '39, '41, and '46 parties, I was able to study the Moenkopi firsthand and to discover in it some of the trackways comprising the subject matter of this paper.

The collection of Moenkopi trackways in the Museum of Paleontology constitutes a valuable but unwieldy record of a good many hundred square feet of Lower Triassic mudflats. The collection is by far the most representative that has been taken from the Moenkopi. It is especially rich in species of *Chirotherium* and is probably qualitatively equal at least to the total representation in European collections from the Bunter and Keuper.

In Europe the smaller types of *Chirotherium* and other small reptiles have not attracted much notice although they are abundant (Lilienstern 1939). Apparently too much has depended on discovery and collection by laymen from commercial stone quarries. In Europe these apparently provide the principal exposures of the Triassic beds. In Arizona and Utah, by contrast, there are thousands of square miles of excellent exposures of gently dipping, redbeds of Lower Triassic age. The underside of almost any sandstone ledge may have a cast impression of an old stream channel or mudflat, some of which are traversed by trackways of vertebrates long extinct.

ACKNOWLEDGMENT

The present study was done under the guidance of Dr. C. L. Camp, Director of the Museum of Paleontology at the University of California. Other persons to whom I am indebted are: Dr. S. P. Welles, of the Museum of Paleontology, for his enthusiastic coöperation in the field—a coöperation which contributes much to the excellence of the trackway collection; Mr. E. D. McKee and Major L. F. Brady of the Museum of Northern Arizona for loan of material, gift of photographs, and timely assistance on certain field problems; Dr. R. C. Stebbins, of the Museum of Vertebrate Zoölogy at the University of California, and Dr. J. R. Slevin, of the California Academy of Sciences, for access to collections in their charge; Drs. A. H. Miller, R. B. Stewart, R. A. Stirton, and Howel Williams for helpful criticism; my sister, Miss Madeline Peabody, and

Mr. Owen Poe for assisting with the preparation of manuscript and illustrations, respectively. Funds generously provided by my father, Mr. Van W. Peabody, Sr., made it possible for me to revisit critical localities in the summer of 1946.

I have made all drawings and photographs unless stated otherwise.

METHOD

An attempt is made to describe a fauna represented by trackways of amphibians and reptiles which inhabited the region now known as Arizona and Utah during the early part of the Triassic period. The amphibians are well represented by skeletal remains but their trackways are scarce. By contrast, the reptiles are poorly represented by skeletal remains, but their many trackways crisscross a number of mudflats which were perfectly cast by subsequent sedimentation. By close study of the pedal morphology exhibited in the trackways, it is possible to gain a surprisingly clear conception of these early Triassic vertebrates. Besides, the reptile trackways contribute an important chapter on a critical period in the history of the Archosauria.

Another discovery made possible a more thorough understanding of some of the basic problems of interpreting the Moenkopi material. A Lower Pliocene plant locality on the flanks of the Sierra Nevada in east central California also yielded excellent trackways of genera from three living families of salamanders, the Salamandridae, Ambystomidae, and the Plethodontidae (Peabody, 1940). These made it possible to compare the trackways of Pliocene vertebrates with those of relatively unchanged, living descendants. Trackways, separate foot impressions, and pertinent measurements were obtained from many living species of salamanders from the Pacific Coast and from the southern Appalachian Mountains. In addition, footprints and measurements were obtained from several pickled species from Asia and Europe. Records of a total of 45 species representing 20 genera are now in the Museum of Paleontology. To complete the study it was fortunately possible to examine a series of natural mudflats on the San Francisco Peninsula and there to identify by their trackways the local salamander fauna—species of *Triturus*, *Ensatina*, *Aneides*, and *Batrachoseps*.

The study of trackways of living Amphibia has given a substantial background for the description of fossil forms. Although a comparable study of living reptiles could not be made in the time available, it is believed that a knowledge of trackways made by primitive tetrapods such as the Caudata constitutes a major step in the understanding of trackways of higher vertebrates.

In the study of trackways recorded by any living tetrapod it is possible to distinguish trackway characters which portray the anatomy of the animal from those which tend to obscure the portrayal. The latter kind may be termed "extramorphologic" and includes characters arising from the type of recording material and from the gait and variable speed of the animal. A trackway, then, exhibits a mixture of morphologic, sedimentary, and dynamic characters. All are important; but if the morphologic characters are not clearly differentiated from the others, a trackway has little significance.

The only trackways to be described are those which are clearly impressed and as free as possible from extramorphologic characters. Considerable effort was made to obtain a large number of consecutive footprints so that their composite detail would provide a picture of the pedal morphology and their arrangement in the trackway would clearly demonstrate the gait and general body form.

For photographic purposes, the surface surrounding footprints was sometimes given a neutral color. A water-soluble paint was suitable. The compass directions were determined in the field whenever possible and are given on diagrams of trackway surfaces, "east" and "west" being reversed there because a cast surface reverses the impression of the original mudflat surface.

Differentiation of vertebrates by their pedal characters must be on a generic level relative to living faunas even though the binomial system of nomenclature is followed. For example, the eight chirotheriid species described here, under the single genus *Chirotherium*, in all probability represent eight different genera. A vertebrate fauna based on fossil trackways must be evaluated with this in mind.

GLOSSARY

As few new terms as possible are used; except for the coined term "hypex," all the terminology is drawn from words in common use. However, these are given restricted meanings. For purposes of clarity the terminology is also illustrated in figure 1.

Impress.—The word "impress" or "impression" is used whether the trackway is preserved in the original (positive) or in the cast (negative). It is a plane surface which is impressed, so if one understands to begin with that the footprint is either the original or the cast, he may use "impress" or "impression" for either. Cast trackways can be studied more conveniently than the original.

Trackway.—For practical purposes, three or more consecutive steps constitute a trackway. With only two consecutive steps the midline and relative width of the trackway can only be estimated from the relative orientation; with one step the entire trackway pattern is missing.

Trackway pattern.—The spacing and orientation of footprints in the trackway, including a tail mark if present, constitute the trackway pattern. The natural pairing of manus and pes impressions in a quadrupedal trackway is referred to as a "set of impressions."

Stride (German—Einseitiger Schritt, Doppelschritt).—A stride, by dictionary definition, is a cycle of movements completed when a foot regains its initial starting position, or it is the distance traversed in such a movement. Of course, the movement is parallel to the direction of progress or to the midline of the trackway pattern. Stride and pace are often confused with each other in ichnological literature.

Pace.—By usage, a pace is the distance between consecutive left and right, or right and left steps of a walking man. The distance, which averages about three feet in man, is measured on a diagonal line which in man is approximately the direction of progress.

Pace angulation.—Any three consecutive footprints form an angle, with the

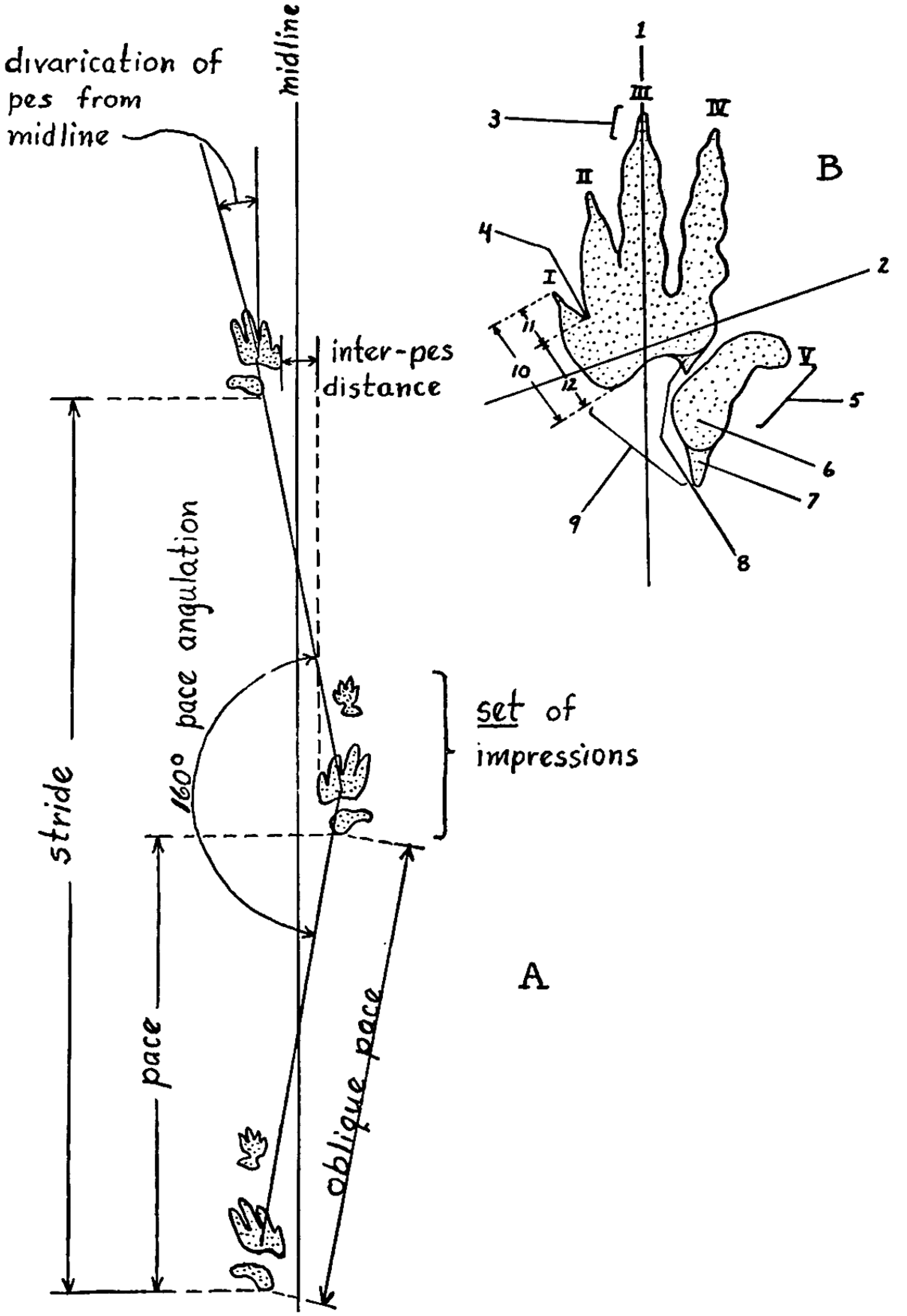

Fig. 1. *A*, the trackway pattern. *B*, pes of *Chirotherium minus* showing characters of the impression: 1, long axis; 2, cross axis or metatarsal-phalangeal axis; 3, claw impression; 4, hypex; 5, phalangeal portion of the fifth digit; 6, metatarsal-phalangeal pad; 7 and 8, metatarsal ridges; 9, metatarsal region; 10, length of digit; 11, free length; 12, communal length.

apex at the middle footprint. This is the angulation of the pace or the pace angulation. The base of digit III is the best reference point from which to determine the exact angle. Preferably the pace angulation should be an average of several consecutive angles made by successive *pes* impressions.

The pace angulation as calculated in degrees is a simple expression of the relative width of a trackway and is independent of other measurements. Heretofore relative width has been expressed, if at all, by unwieldy combinations of linear measurements.

Hypex.—The apex of the reëntrant angle between digits.

GEOLOGICAL OCCURRENCES

The Moenkopi Formation of the Little Colorado Valley

In the valley of the Little Colorado River there are extensive exposures of predominantly red sandstones and shales, the "Moencopie" formation of Ward (1901). Originally assigned to the Permian, these strata are now considered to represent the early part of the Triassic. Unconformable relations with the underlying Kaibab and Coconino formations and with the overlying Shinarump, and the presence of invertebrate faunas in marine phases of the Moenkopi, provide evidence for the correlation. Much of the vertebrate evidence is contained in collections of the Museum of Paleontology of the University of California and is being described by Dr. S. P. Welles. Stegocephalian amphibia in the Upper Moenkopi near Holbrook, Arizona, indicate a general correlation with the German Bunter and perhaps with part of the Keuper (Welles, 1947).

The Moenkopi formation is widespread in the southwestern United States. Undoubtedly it was laid down in part of a great depositional province in western North America. A Pacific sea extended through northern and eastern California into Nevada, Utah, southern Idaho, western Wyoming, northern Arizona, and possibly western New Mexico. Although purely marine in the western part of the province, the Lower Triassic deposits change until they are dominantly terrestrial along the eastern borders, in Wyoming, Utah, and especially in Arizona. The paleogeographic map (fig. 2) is an attempt to bring that of Schuchert (1910) up to date in the light of much subsequent stratigraphic work by Darton (1925), Gregory (1917, 1938), Gregory and Moore (1931), Longwell (1928), Gilluly and Reeside (1928), Baker (1936), Harrel and Eckel (1939), Nolan (1943), and many others, including members of Museum of Paleontology field parties.

The variegated sandstones and shales of the Moenkopi have been described minutely from many areas where nearly vertical sections are common. However, the area between Cameron and Holbrook, where most of the vertebrate remains have been found, is characterized by uncapped remnants of the formation. These seldom afford a complete section. The area of exposure broadens from a few miles near Cameron to 30 miles south of Holbrook. The strata have a slight regional dip to the northeast over most of the area. Northwest of Cameron the dip steepens on the flank of the East Kaibab monocline.

South of the Little Colorado River there are only two complete sections, one near Cameron and one in the Moqui Wash area west of Winslow. A section of the lower half of the Moenkopi was compounded from separate stations in Moqui Wash (figs. 5 and 6); it illustrates a typical lithologic succession of the Moenkopi. Cross-bedded sandstones and scattered conglomerates, which rapidly vary laterally, alternate with evenly bedded shales, usually maroon in color.

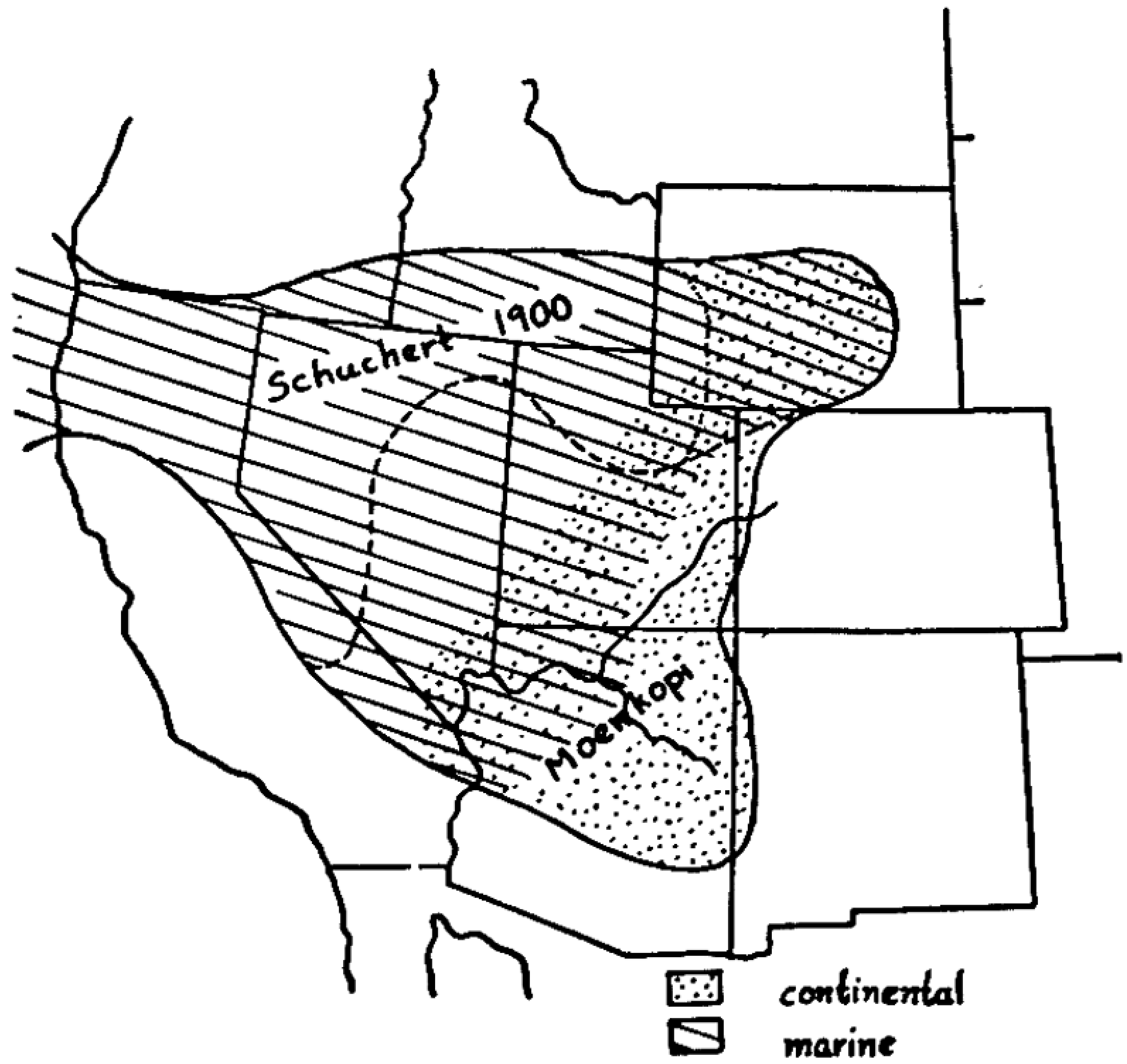

Fig. 2. Lower Triassic province of deposition in western United States, generalized to show relation of marine to continental facies.

A persistent medial zone of gypsiferous shale occurs in the Moenkopi between Cameron and Holbrook. Since no trackways or bone seem to occur in this zone but are present above and below, the Moenkopi can be conveniently divided into pregypsum, gypsum, and postgypsum stages. These are referred to here as the Lower, Middle, and Upper Moenkopi, respectively, following Welles (1947). Vertebrate faunas could be expected to show some differences between the lower and higher levels, which are separated by an estimated 100 feet of variegated shale, sandstone, and gypsum.

A persistent massive sandstone, which weathers into rounded shapes, occurs at or near the base of the formation between Cameron and Winslow. No vertebrate fossils have been found below it or in it, but lenses of sandstone immediately above may contain reptile footprints (fig. 8, *A*).

Trackways generally do not provide as sound a basis for correlation as do skeletal remains. However, the trackways of *Chirotherium*, the "hand animal" of the Triassic, may be an exception. Chirotheriids are well represented in the Lower and Upper Moenkopi, but in the German Bunter they occur mainly in the Upper, sparingly in the Middle, and not at all in the Lower (Soergel, 1925).

They are also well represented in the Middle Keuper[1] and perhaps even in the Upper Keuper of England (Egerton, 1839); and are known from the Italian Keuper (Huene, 1941). A single set of poorly impressed footprints from the Upper Triassic of eastern United States indicates that *Chirotherium* lived after Moenkopi time in North America. The typical and most common species, and also the oldest known, *C. barthi*, occurs in the Upper Bunter of Germany and in the Upper Moenkopi of Arizona.

Origin of the Trackway-bearing Surfaces

It has been concluded by Twenhofel (1926, p. 177) that "redbeds were deposited in a subaerial environment in which fluvial deposition was most important [lacustrine deposition of secondary importance], the deposition taking place under climatic conditions which were semi-arid or at least less humid than the places where such sediments originated." Certainly a salient character of the Moenkopi redbeds is the great number of ripple marks, channels, and desiccated mudflat surfaces associated with deposits of fluviatile sandstones and conglomerates. Recent discoveries of bones and trackways of terrestrial vertebrates in sandstones and conglomerates and in shales closely associated with them, are conclusive proof of fluvial deposition during Moenkopi time.

The contours of channel bottoms and mudflat surfaces show clear evidence of flowing water and of the direction of flow. Such evidence is so plentiful that a detailed study would furnish valuable data on the orientation of Moenkopi rivers. For example, some channel bottoms show potholes and current scouring made by streams several feet deep. One of these channels, eroded in red, laminated mud and cast by infilling sand is shown in plate 25, *B*. The flow of water from left to right is clearly indicated. The following observations are restricted to indications of fluvial deposition shown on the mudflat surfaces which contain vertebrate trackways.

Cast surfaces of Moenkopi mudflats often show scattered, small crescent-shaped impressions like those commonly left by ebbing streams of water on recent fluvial mudflats. These impressions are formed in shallow water which eddies around small obstructions such as pebbles, seeds, or bits of wood. The "horns" of the crescents point in the direction of the current. In the Moenkopi, flat pebbles of dried mud, apparently derived from upstream mudflats, produced these "current indicators." Details of a current indicator cast in sandstone are shown in plate 24, *B*. The original pebble of dried mud weathered away, leaving a cavity, a latex cast of which shows that the pebble was flat with rounded edges, and had been left on a small pedestal formed by the eddy. The pebble responsible for the current indicator is often enclosed and preserved in the overlying sandstone. Composition and contour of the pebble can be determined by breaking the sandstone through the cast impression of the current indicator.

Although current indicators are common on mudflats of recent streams, their fossil equivalents may not be recognized. A cluster of current indicators shown

[1] According to Dr. D. M. S. Watson (letter, March, 1947), *Chirotherium* in England "may be Keuper but it might equally well be of Muschelkalk age, or indeed anywhere you like in the Trias."

in plate 45 accidentally resembles the pattern of a vertebrate trackway. Indeed, Willruth (1917) and Walther (1917) describe isolated horseshoe-shaped "tracks" from the German Bunter and consider them to be the heel marks of *Chirotherium*.

The dry, cracked layer from mudflats apparently provided most of the shale pebbles in the conglomeratic foreset beds of the Moenkopi. The impression of a capitosaur skull shown in plate 24, *A*, illustrates how vertebrate remains sometimes occur in foreset beds composed mainly of flattened pebbles of shale. Origin of the pebbles is suggested by a recent fluvial mudflat on the bank of the Russian River, California (pl. 26, *A*), where the thin layer of mud was baked into brittle, loose plates which easily could have been transported downstream with the next high water, to be deposited as flattened pebbles. In this connection, cross sections of some Moenkopi mudflats show that peripheral areas of the dried and cracked mud were disturbed by the renewed current of water which deposited the overlying sandstone.

Evidence of salinity, such as pseudomorphs of salt crystals, have only been observed in association with vertebrate trackways at one locality, namely in the Upper Moenkopi northwest of Cameron (loc. V4208), where the pseudomorphs are associated with the cast footprints of lacertoid reptiles. The pseudomorphs indicate evaporation of a standing body of water, possibly a brackish pool.

The Russian River mudflat also demonstrates an optimum condition for recording clear vertebrate trackways; namely, a thin layer of fine-grained mud deposited on a relatively firm, sandy layer. Of course, the vertebrate must walk on the mud at an appropriate time. For example, a wading bird (bittern) and a mammal (raccoon) crossed trails on this mudflat (pl. 26, *B*). The bird traversed the surface just before or soon after the water had receded, so that the detail of the footprint is not clear. Some time later, but before an advanced stage of desiccation, the mammal crossed the surface and left an exceptionally clear trackway. The best Moenkopi trackways were apparently made under similar conditions. It is interesting to note that this mudflat was almost completely devoid of any evidence to indicate the diversity and abundance of the surrounding flora.

Vertical successions of mudflats like the one observed on the Russian River occur in the Moenkopi. A roadcut on the Flagstaff–Cameron highway (pl. 25, *A*) shows a series of thick lenses of sandstone separated by thin lenses of shale. Most of the latter show evidence of subaerial exposure. The surface of one lens received the clear footprints of a throng of large and small reptiles. As in the best Moenkopi trackways, the overlying sandstone preserved the detail of the original surface (pl. 43, *A*). The more resistant sandstone retains the cast impression of the original mudflat surface long after the shale has disintegrated. Perhaps the most perfect example of this type of preservation is shown by the sandstone slabs in plate 37. At the time of their discovery, a brush of the hand removed all that remained of the original shale surface. A few tracks have been found impressed in what were originally sand surfaces, but these tracks usually lack essential details of the foot.

One of the most interesting Moenkopi mudflats occurs near Meteor Crater (fig. 21). Here, the trackways were recorded on a thin layer of white calcareous marl and preserved by a sandy limestone. In the laboratory, quantities of the mud still adhering to the limestone were softened and washed off with water. The mud apparently exhibited the same characters in the laboratory that it had on the Triassic mudflat because it was used successfully to record excellent

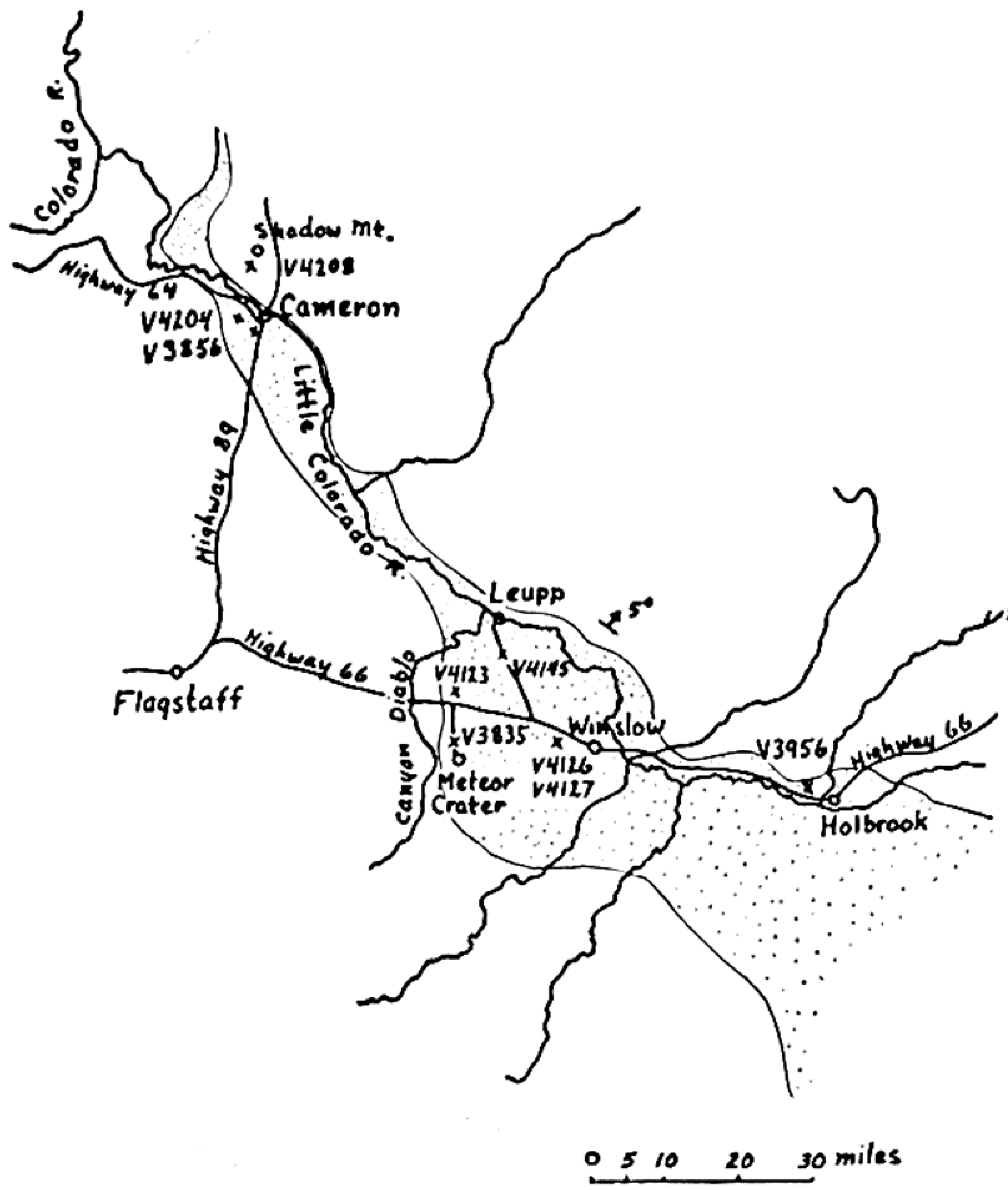

Fig. 3. Trackway localities in the Moenkopi formation of Arizona.

trackways of a number of living species of North American salamanders (pl. 28, *B*). Allowed to dry, the mud developed a crack system similar to that observed on the fossil mudflat (pl. 26, *C*).

Localities and Material

The important localities in the Lower Moenkopi are Meteor Crater and Moqui Wash; in the Upper Moenkopi they are Cameron and Penzance. All are in Arizona. Other localities for the most part have produced isolated footprints and mudflat phenomena. With few exceptions all known vertebrate trackways and footprints from the Moenkopi are in the collections of the Museum of Paleontology of the University of California. The exceptions are: three isolated pes impressions of *Chirotherium barthi* mounted in the walls of the hotel lobby at Cameron; a trackway of three consecutive steps of *C. barthi* at the Naturalist's Workshop, Grand Canyon National Park (south rim); two excellent trackways and numerous isolated footprints of *C. barthi*, and footprints of

Rotodactylus at the Museum of Northern Arizona, in Flagstaff. All these specimens were collected in the Upper Moenkopi southwest of Cameron, and from the same zone which yielded the Museum of Paleontology specimens. Trackways of *Chirotherium barthi* are as common in this region as at the type locality in Hessberg, Germany.

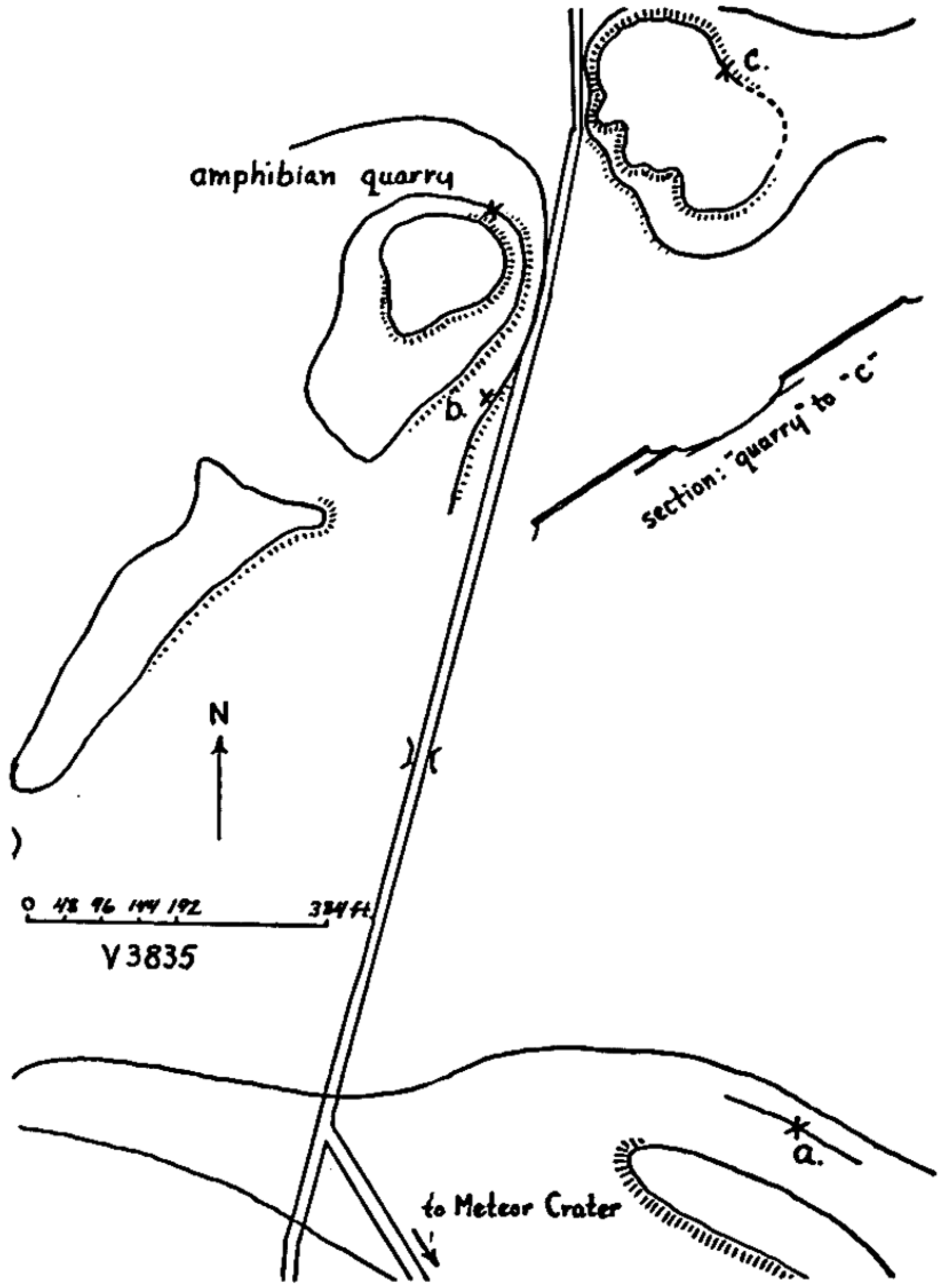

Fig. 4. Map showing trackway localities at Meteor Crater, loc. V3835.

METEOR CRATER, ARIZONA (U.C.M.P. LOC. V3835)

Locality.—Trackways occur at about the same level in a series of low buttes in the Lower Moenkopi just north of Meteor Crater (fig. 4). The fossil-bearing horizon is about 50 feet above the contact with the Kaibab limestone.

Material.—1. From "amphibian quarry" (fig. 4), a series of 31 slabs (fig. 21), and a series of 3 slabs (fig. 29) preserving part of an extensive mudflat upon which occur the crisscrossed trackways of *Chirotherium* and of a small "spur-footed" reptile, *Rotodactylus:* also many isolated footprints from the same surface. 2. From "*a*," a series of 15 slabs (figs. 16, 17) showing mud-crack pattern and trackways of *Chirotherium* and of *Rotodactylus;* also many isolated footprints of *Rotodactylus*. 3. From "*b*," a set of footprints of *Chirotherium*

(fig. 30, *A*) and casts of coprolites and plants. 4. From "*c*," one slab with numerous footprints of *Chirotherium* (nos. 37334, 37776).

A locality of minor importance occurs one mile north of the Meteor Crater road junction with State Highway 66, in a low butte (V4123, fig. 8, *A*). Isolated footprints of lacertoid reptiles were collected here (fig. 15). *Chirotherium* also occurs.

MOQUI WASH, ARIZONA (U.C.M.P. LOC. V4126, 4127)

Locality.—Trackways occur in the Lower Moenkopi in a zone approximately 70 feet above the contact with the Kaibab limestone (figs. 5, 6).

Material.—Loc. V4126: One set of footprints of a giant *Chirotherium* (fig. 26), the manus and pes occurring on separate blocks; three slabs with a maze of small reptile tracks. These specimens come from only a small part of an extensive mudflat surface preserved by a thick sandstone which outcrops around the perimeter of a small butte. The sandstone bears upon its upper surface the positive digit tip impressions of capitosaurid amphibians. A short distance to the north, the same sandstone produced the articulated skeleton of a capitosaur (fig. 10).

Loc. V4127: Two slabs containing isolated sets of amphibian footprints (fig. 9, pl. 27).

In the western part of section 25, at "x," occur trackways of a giant chirotheriid related to that from loc. V4126, but these have not been collected. In the eastern part of section 25, at "x," occur trackways of *Chirotherium* and of lacertoid reptiles; these also have not been collected (pl. 55).

CAMERON, ARIZONA (U.C.M.P. LOC. V3856, V4204, V4208)

Locality.—A complete section of the Moenkopi formation is exposed southwest of Cameron on the flank of the East Kaibab monocline. Here, trackways of *Chirotherium* occur in an area of several square miles and in a zone in the Upper Moenkopi which is about 60 feet below the contact with the overlying Shinarump conglomerate.

Material.—Loc. V3856: One large slab from part of an extensive mudflat surface exposed in a roadcut 6 miles south of Cameron on the Flagstaff–Cameron highway (pls. 25, *A*, and 43); a series of 10 slabs from the same level but one mile northwest of the roadcut, and just west of a stone quarry (figs. 24, 25).

Loc. V4204: Two large slabs from a widespread mudflat surface exposed near the top of a west facing butte, one mile south of the Grand Canyon Highway, 2 miles west of its junction with the Flagstaff–Cameron highway (pl. 40).

Slabs from these two localities provide an excellent record of *Chirotherium barthi* and of two new species of *Chirotherium*. Lacertoid footprints also are numerous but they do not lend themselves to description.

Loc. V4208: A locality of minor importance was found 7 miles northwest of Cameron in the Upper Moenkopi, between Shadow Mountain (Black Butte) and the Little Colorado River. Three slabs containing trackways of lacertoid reptiles were collected here (pl. 29).

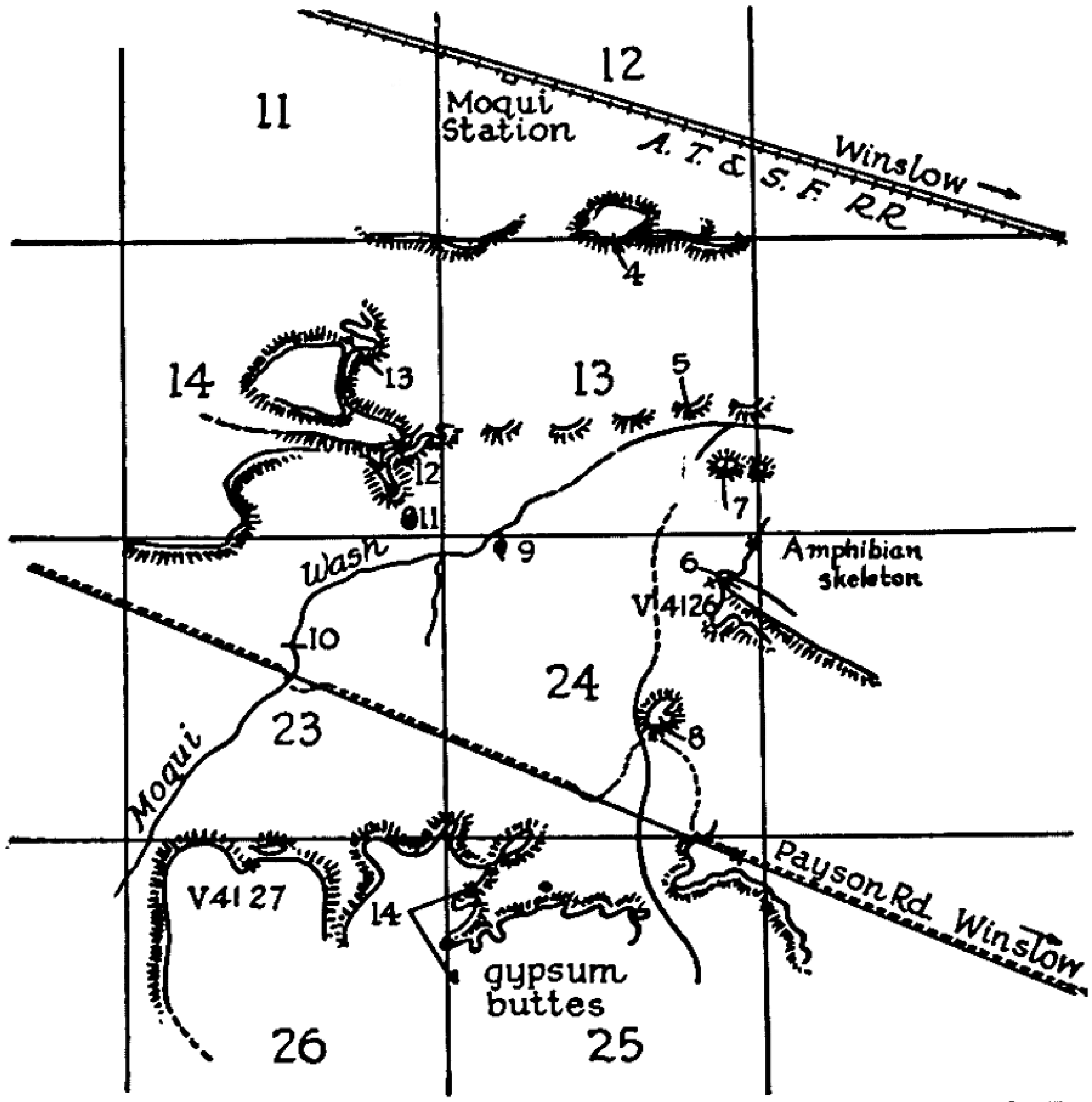

Fig. 5. Map showing location of geologic sections taken in Moqui Wash, and trackway localities.

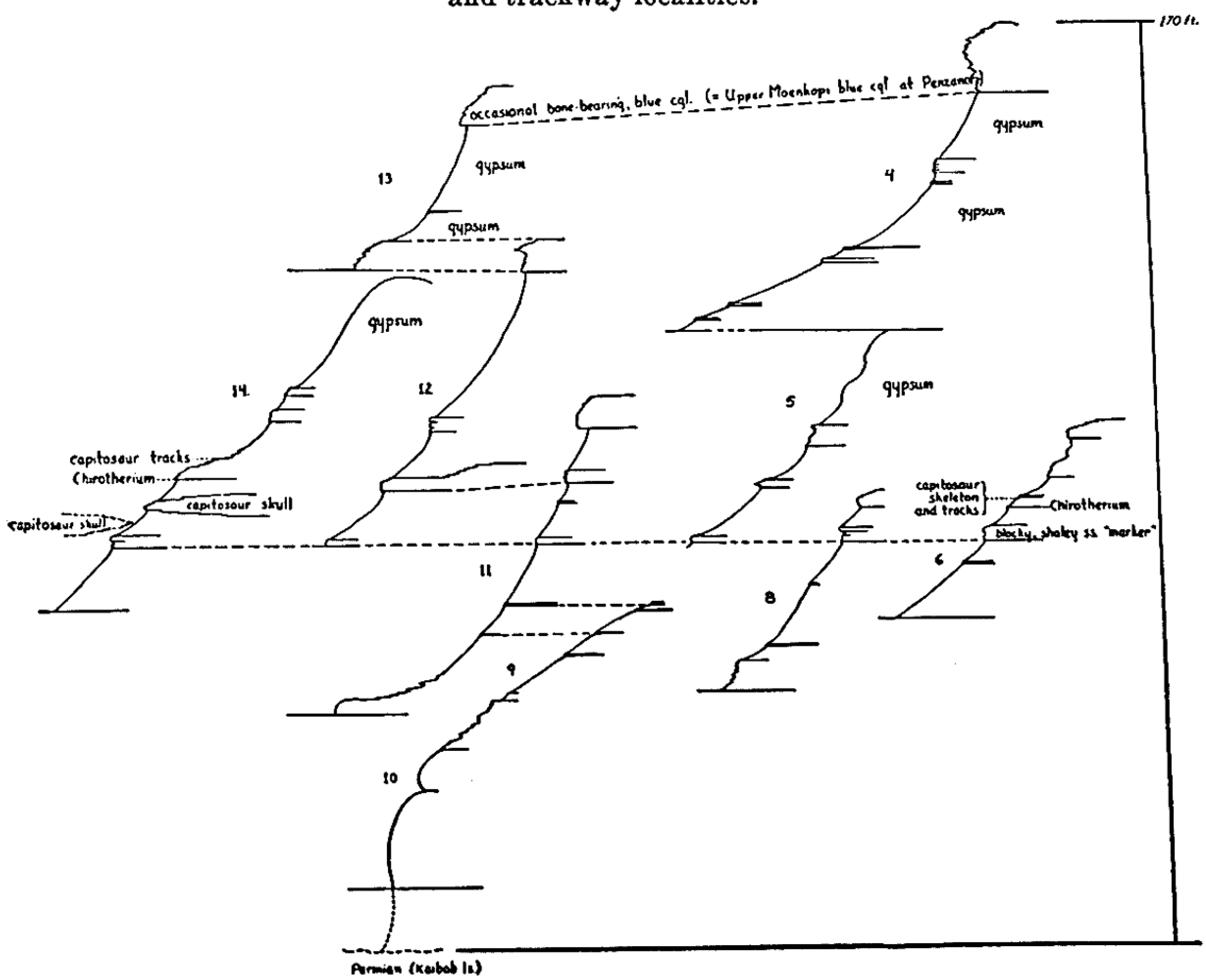

Fig. 6. Sections in Moqui Wash showing the lower half of the Moenkopi formation with massive ss. at base overlain by alternating sandstones and shales, gypsiferous in part.

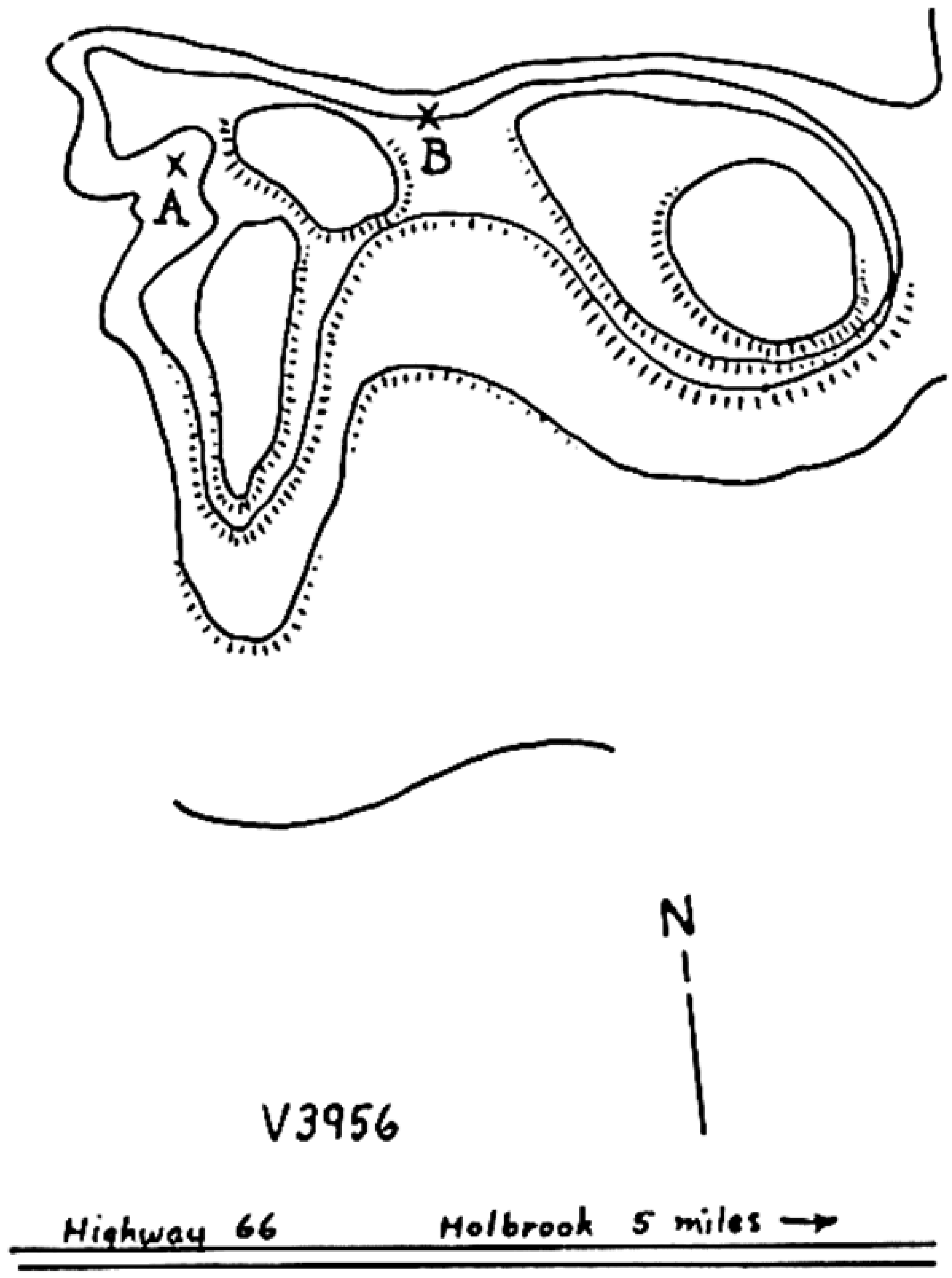

Fig. 7. Map showing trackway localities in low, connected buttes north of Penzance station.

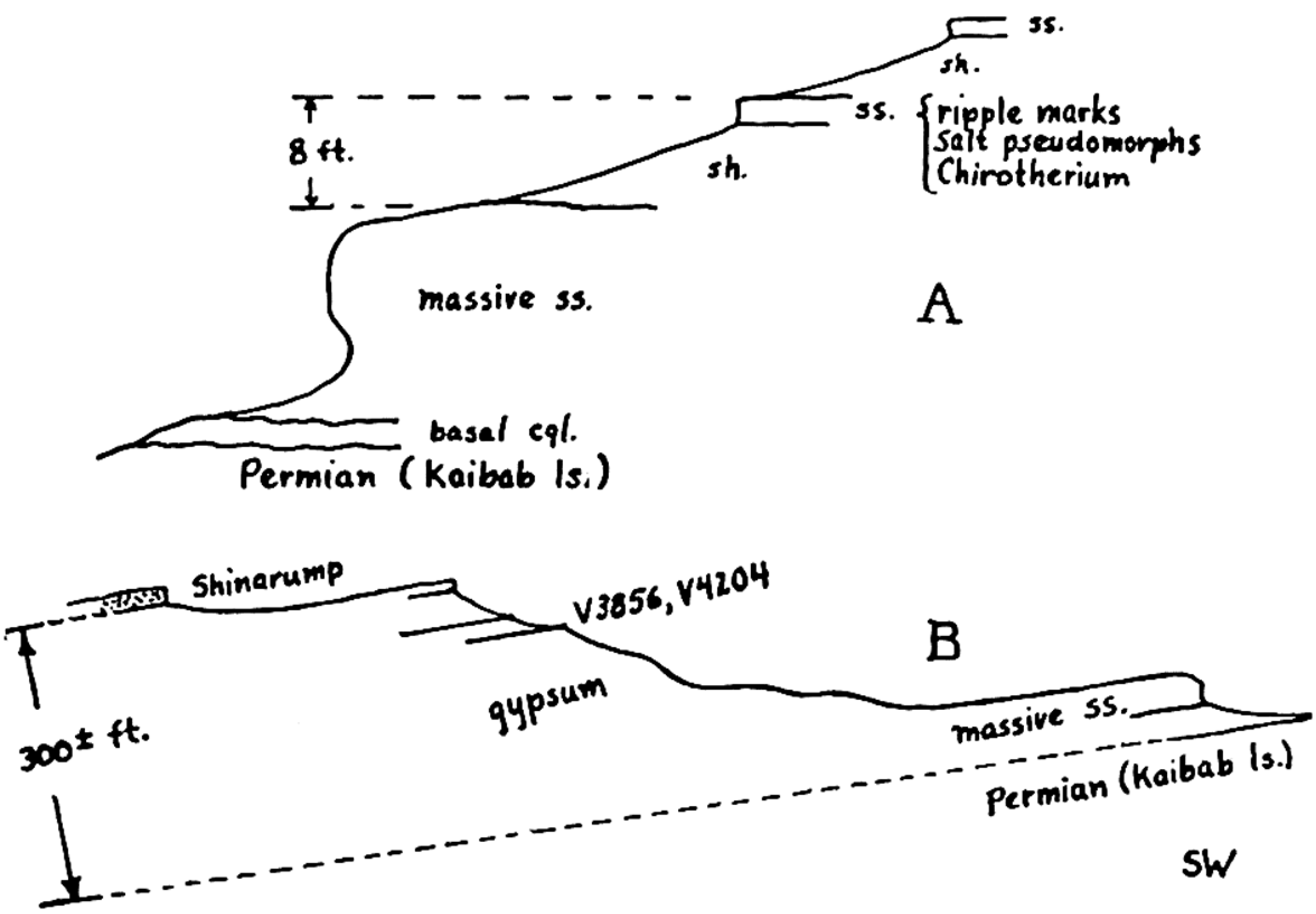

Fig. 8. *A*, basal section in Moenkopi formation north of Meteor Crater, loc. V4123. *B*, northeast-southwest section through the Moenkopi formation south of Cameron.

PENZANCE, ARIZONA (V3956)

Locality.—Trackways occur in the Upper Moenkopi in a series of low, connected buttes just north of State Highway 66, 1.5 miles north of Penzance Station (Santa Fe R.R.) and 5 miles west of Holbrook (fig. 7). The trackway horizon is approximately 130 feet above the contact with the Coconino formation and well above the middle gypsiferous zone of the Moenkopi.

Material.—Four slabs (fig. 31, *A*) from part of an extensive mudflat surface (fig. 31, *A*), containing footprints of a species of small-manus *Chirotherium* (fig. 30, *B*).

A trackway showing this species in an arrested position (fig. 31, *B*) occurs at about this same level (fig. 7, *A*) but was not collected.

HURRICANE, UTAH (U.C.M.P. LOC. V4602)

Locality.—Trackways are present in a roadcut 8 miles west of Hurricane on State Highway 17, where it crosses the eroded west limb of a northeast–southwest trending anticline. The level is in upper Moenkopi beds approximately 25 feet below the contact with the overlying Shinarump sandstone, and extends for a distance of about 20 feet along the roadcut.

Material.—Three slabs totaling about 3 square feet of the trackway surface, containing many footprints of the "spur-footed" reptile, *Rotodactylus* (pls. 31, 32).

ROCKVILLE, UTAH (U.C.M.P. LOC. V4603)

Locality.—Trackways were found on the west side of a small canyon immediately north of the Rockville village cemetery. The trackway surface is exposed in a sandstone cliff in upper Moenkopi beds about 60 feet below the contact with the overlying Shinarump sandstone.

Material.—Two slabs found on the talus slope, containing isolated footprints of a giant *Chirotherium* (pl. 41).

VALLEY OF FIRE, NEVADA

Longwell (1928, p. 45) reports "tracks of small reptiles" in the middle of 1,598 feet of Moenkopi strata in the Valley of Fire opposite Logan Wash in southern Nevada. A more exact locality and description of these tracks is not available at this time.

FAMILY CAPITOSAURIDAE (AMPHIBIA: LABYRINTHODONTI)

Footprints

Amphibian trackways have not been found in the Moenkopi formation, but isolated footprints occur at three localities in the Lower Moenkopi of Moqui Wash. These have a special interest because they are present at a horizon (fig. 6) which produced the articulated skeleton of a capitosaurid amphibian. This coincidence is so rare that opportunity is taken to describe the isolated footprints in detail and to relate them as far as possible to the capitosaurid.

The footprints occur as positives in laminated, silty sandstone. Parts of the

footprint-bearing surface show faint ripple marks. The locality (V4127, fig. 5) is in Moqui Wash about two miles southwest of where the capitosaurid skeleton was found, and at about the same horizon. Obscure footprints and isolated digit tip impressions, not described here, were observed near by on ripple marked surfaces associated with the skeleton and at the same horizon (V4126).

No. 37759 (fig. 9, pl. 27, *A*)

The clearest set of footprints consists of two arc-shaped series, one behind the other, of rounded impressions. Each rounded impression was made by the bluntly rounded, clawless digit of the amphibian foot. The sand is shoved back into a posterior ridge around the deeper impressions and toe dragmarks lead

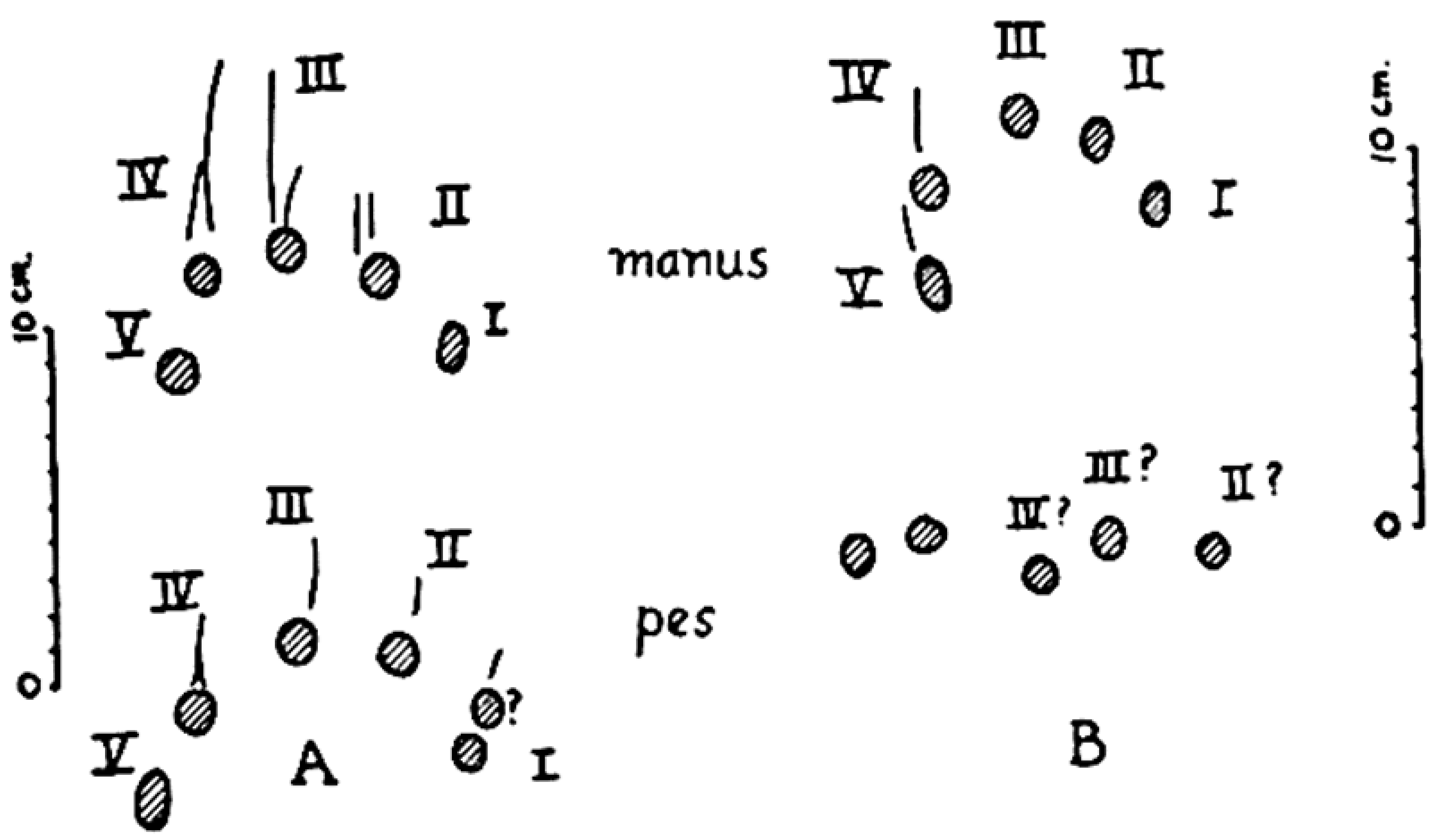

Fig. 9. Diagram of capitosaurid footprints shown in pl. 27: *A*, no. 37759, manus and pes; *B*, no. 37760, manus and ? pes.

away anteriorly. The disposition of pressure ridges and toe dragmarks indicates that the arc of impressions is convex in the direction of progress, and that the arcs, one behind the other, represent a normal set of manus and pes impressions of a tetrapod trackway.

The digit tips tend to be impressed slightly deeper on one side (the right side here), which normally is the median side in trackways of primitive tetrapods. Also, the short toe dragmarks of the pes are very slightly curved with the convexity toward the side of strongest impression, a character reflecting the lateral movement of the hind leg of primitive tetrapods away from the midline.

Pes.—The slab is a very thin friable sandstone which broke in transport and a small piece bearing part of the faint elongate mark of digit V is missing. Reference is actually to the tip of the digit only since all the amphibian tracks from the Moenkopi formation show nothing but digit tip impressions. A drawing made in the field supplies the missing detail. Digit IV made a very shallow depression but left a furrow 2 cm. long during retraction so that its impression can be located accurately. Digits II and III are strongly impressed; II pushed back an amount of sand about equal to its area of impression. Narrow retraction furrows 2 cm. long lead away anteriorly from the median side of the digit impressions. The medial displacement of the furrows relative to the digit tip impressions agrees with the amphibian method of retracting the pes while walking (Schaeffer, 1941). The impression of digit I is confused by two

marks, one behind the other. The posterior one is taken to represent the mark of the digit because it makes an arc with the other four impressions more in accord with the generalized pes of living salamanders and with the foot of the capitosaurid skeleton from the Moenkopi. The arc of five impressions has a radius of about 5 cm. Other measurements are given in table 1.

TABLE 1

MEASUREMENTS OF CAPITOSAURID FOOTPRINTS, FOSSIL AND RECONSTRUCTED, AND OF THE RECONSTRUCTED FOOT (in centimeters)

	Fossil footprints			Capitosaurid skeleton		Reconstructed footprints of a capitosaurid	
	No. 37759	No. 37760					
	Manus	Pes	Manus	Manus	Pes	Manus	Pes
Max. width:							
I–IV	8.5	9.0	7.3	5.0	6.1	5.0	6.5
I–V		10.0	7.8	5.5	7.0	6.0	7.7
Max. length:							
I–IV	3.0	3.7	3.4	1.6	2.0	2.2	2.6
I–V	...	5.0	4.8	2.5	3.3	2.9	3.7
Separation of digit tips, center to center:							
I–II	2.8	3.4	2.5	1.5	2.1	1.6	2.5
II–III	3.0	3.0	2.6	1.7	2.0	1.8	2.4
III–IV	2.9	3.7	3.5	1.7	2.0	1.9	2.1
IV–V	...	2.3	2.9	1.6[a]	2.4	2.0	2.7

[a] 1.8 cm. on shorter reconstruction of V.

Manus.—An arc of impressions with a radius of 5 cm. occurs 10 cm. anterior to the pes and consists of only four certain impressions of digit tips. These are taken to be the marks of digits I–IV because of the orientation with the pes and because of evidence from another similar manus described below. Digit V apparently failed to impress the sand although there is a very faint disturbance in the surface posterior to digit IV. The manus of specimen no. 37760 shows more clearly the mark of digit V. Digits II–IV are all strongly impressed and medioposterior pressure ridges rim the impressions. Shallow retraction furrows lead away anteriorly from the lateral side of the impressions of digits II and III, thereby contrasting with the pes. The furrows are longer than those associated with the pes: 2 cm. for digit II, 5 cm. for III, 6 cm. for IV. In front of digits II and III the furrows are peculiarly doubled as if a relatively large area of the retracting digit scraped the ground.

The manus was somewhat smaller than the pes and in the proportion of about 8 to 10. A line drawn through digit III of manus and pes should be approximately parallel with the center line of the trackway. The nature of the foot impressions, particularly the arc of digit tip impressions with the associated toe dragmarks, suggests strongly an amphibian origin. The manus and pes which made the impressions probably had the following characters: a

pliable, supple foot with no definite posterior limit to palm or sole, hence no specialized tarsal or carpal joint; digits somewhat variably spaced relative to each other but showing no marked offset of the outer digit; digits more or less radiating forward from the carpal and tarsal region within an angle of 90 to 100 degrees; digit tips blunt, clawless, and depressed while emplaced during locomotion.

The relation of the manus and pes to each other indicates that the animal was fairly short bodied, that is the glenoacetabular distance was either equal to or somewhat less than the sum of the length of fore and hind limb—living salamanders being used as a criterion. The relative position of manus and pes together with the disposition of pressure ridges and toe dragmarks indicates that the manus regularly occurs just in front of the pes and about as far from the midline. The slightly smaller manus is more strongly impressed than the pes, suggesting a "front heavy" animal of the stegocephalian type.

No. 37760 (fig. 9, *B*, pl. 27, *B*)

Another thin slab collected from the same place and same level as specimen no. 37759 shows an arc of five digit tip impressions. The arc lies about 10 cm. ahead of what is considered to be a confused muddle of digit-tip impressions, some of which belong to the pes. The arc of rounded impressions is noticeably stronger on the right side, considered to be medial for reasons already stated. Thus digits IV and V are faintly impressed, V having barely brushed the sand into a faint posterior ridge. Impressions of I and III have posterior pressure ridges. Faint, shallow retraction furrows lead away anteriorly from IV and V indicating the general direction of progress and strengthening the view that the pes is represented somewhere in the rounded depressions 11 cm. directly behind manus digit III. The fact that digit V impressed very faintly nearly directly behind the tip of IV would suggest that manus digit V of no. 37759 merely failed to leave a legible record.

The arc of the manus impression has a radius of slightly less than 4 cm. and is therefore smaller than that of the first specimen. The arc is relatively longer indicating a wider angle of radiation of the digits from the carpus.

It is impossible to decipher the cluster of digit-tip impressions behind the manus although some of the impressions probably represent digit tips of the pes. The impression nearest the manus indicates that the minimum separation of manus and pes impressions is probably greater than for specimen no. 37759. However, in view of the incompleteness of both specimens further detailed comparison would be speculative.

A Capitosaurid Skeleton
No. 36713

We may turn now to a description of the capitosaurid skeleton and to the possibility that the footprints described above are capitosaurid in character.

The skeleton is that of a small, perhaps juvenile individual. The originally rather flat body, compressed further by induration, lies in the bedding plane. For this reason a little preliminary preparation has uncovered much detail of

the skeleton. The skull and vertebral column lie in a nearly straight line, the tail curving slightly to the left side. The limbs, except for the left front, which is not exposed, extend laterally and posteriorly in a perfectly natural manner. The total length, length of tail, dorsal and cervical regions, and length of skull are accurately indicated. Also there is little question about the length or position of the limbs with respect to the girdles. The separation of the glenoid fossae is not large in spite of the apparent broadness of the body. The separation of the acetabulae is relatively less than in living salamanders and is about the same as in the labyrinthodont, *Trematops* (Schaeffer, 1941, reconstruction). The tail was apparently compressed but details other than its length are not well exposed.

The articulated skeleton of a labyrinthodont is a rare discovery in itself, but the Moqui specimen possesses in addition to a relatively complete and undistorted skeleton the skin impression and resulting outline of much of the body. Several of the digits are thus outlined partly, the fourth digit of the right pes completely. The skin impression in the dorsal region extends several centimeters laterally from the line made by the ends of the ribs. Possibly there was a lateral flap of skin similar to that of the giant salamander, *Cryptobranchus*. However, flattening of the body by overlying sediments could appreciably widen the area of skin impression. Since the separation of glenoid and acetabular cavities is definitely known to be moderate to narrow for Amphibia, the outline of the dorsal region was reconstructed conservatively a short distance lateral to the line of rib ends. The skin of the hind margin of the hind leg extends into a vanelike flap.

Right and left pes lie in a natural, relaxed position with the sole directed downward and backward. The digits radiate evenly from the tarsus and show little distortion. The right manus as exposed in preparation is complete but distorted somewhat by lateral compression. The digits are not as fully extended as in the pes. Both manus and pes are pentadactyl. Nearly all digital segments can be seen, although the terminal phalanges are tiny flecks of bone. Ultraviolet light determined the presence or absence of bone in case of doubt.

Pes.—The only question concerning the phalangeal formula is whether digit I had 1 or 2 phalanges. Neither pes provides any information except that the proximal half of metatarsus I is robust and hence indicates a well-developed digit. Since the manus seems to have only one phalanx in digit I and since one phalanx is at least as compatible with the disposition and length of all the digits as two would be, the outline of the pes digit I is drawn to conform with the arc formed by the tips of II, III, and IV. The phalangeal formula is thus 1–2–3–3–2, or the same as that of the living salamandrid and plethodontid salamanders.

Skin impressions from the right and left pes delineate all of digit IV; half of V; the depth of the division between III, IV, and V; and the extent of the flesh beyond the terminal phalanges of IV and V. Part of the lateral border of V is also discernible as it passes into the outline of the large flap of skin along the posterior margin of the limb. The actual width of the digits was probably less than drawn although originally the digits probably were relatively flat. The digit tips are clawless and bluntly rounded.

The total angle of radiation of the digits as drawn is about 70 degrees, roughly that of the original specimen. The actual spread of the digits while walking was undoubtedly greater, probably near 90 degrees. There is no indication that digit V is offset from the others. The digits progress in length from I to IV, the tips lying in an arc of 4-cm. radius. Digit V is slightly longer than II and shorter than III. Other measurements are given in table 1.

Manus.—The right manus preserves all the phalanges of the foot but there are no traces of skin impression. The left manus is unexposed. Digit V, unlike that of the pes, has 3 phalanges if a tiny terminal fleck of bone is counted. This makes digit V relatively longer than pes digit V of which the length is indicated by skin impression. Otherwise the proportions of the manus and pes are similar except for the larger size of the pes. The skeletal length of digit III including the metapodial is 3.6 and 4.3 cm., respectively, in manus and pes.

The manus digits are slightly bunched together in the specimen but are drawn so that the total angle of radiation is 70 degrees, an angle probably somewhat greater in the walking animal. There is no evidence that digit V was offset from the others. Other measurements are given in the table.

Cartilage.—The joints between limb and girdle, between bones of the limb and foot, and the carpus and tarsus were cartilaginous. The relatively large amount of cartilage together with the small size of the skull, relative to other specimens, may mean that the skeleton represents a young individual. In spite of the large amount of cartilage, the limbs are not in the least degenerate in size or shape. I agree with Schaeffer (1941), who has studied the locomotion of salamanders, that "there is no reason for believing that the amount of ossification is related to the aquatic or the terrestrial habits of the animal or to its size or weight." There is no evidence that the capitosaurid limbs could not have operated in the normal manner of living salamanders such as *Triturus* to carry the body free of the ground for short distances. The skeletal characters justify the assumption that the walking gait of the capitosaurid was essentially like that of a living primitive tetrapod such as *Triturus*.

Reconstructed Trackway Pattern

Proportional data derived from salamander trackways can be used to determine the probable stride, relative width or pace angulation, and actual width of the capitosaurid trackway pattern. This method gives results which seem at least as accurate as any method which approaches the problem through an analysis of skeletal function. Measurements from trackways of representative members of the three families of terrestrial salamanders, Salamandridae, Ambystomidae, Plethodontidae, may be averaged to obtain the best results. *Ambystoma, Dicamptodon,* and *Aneides* are most representative for characters of the trackway pattern. *Triturus* and *Ensatina* are unique among salamanders in having the longest relative stride and the largest pace angulation. Measurement of the hind limb was taken post mortem from the individual that made the trackway. Plaster casts of the trackways are in the Museum of Paleontology collections; the animals which made the trackways are in the pickled collection of the Museum of Vertebrate Zoölogy.

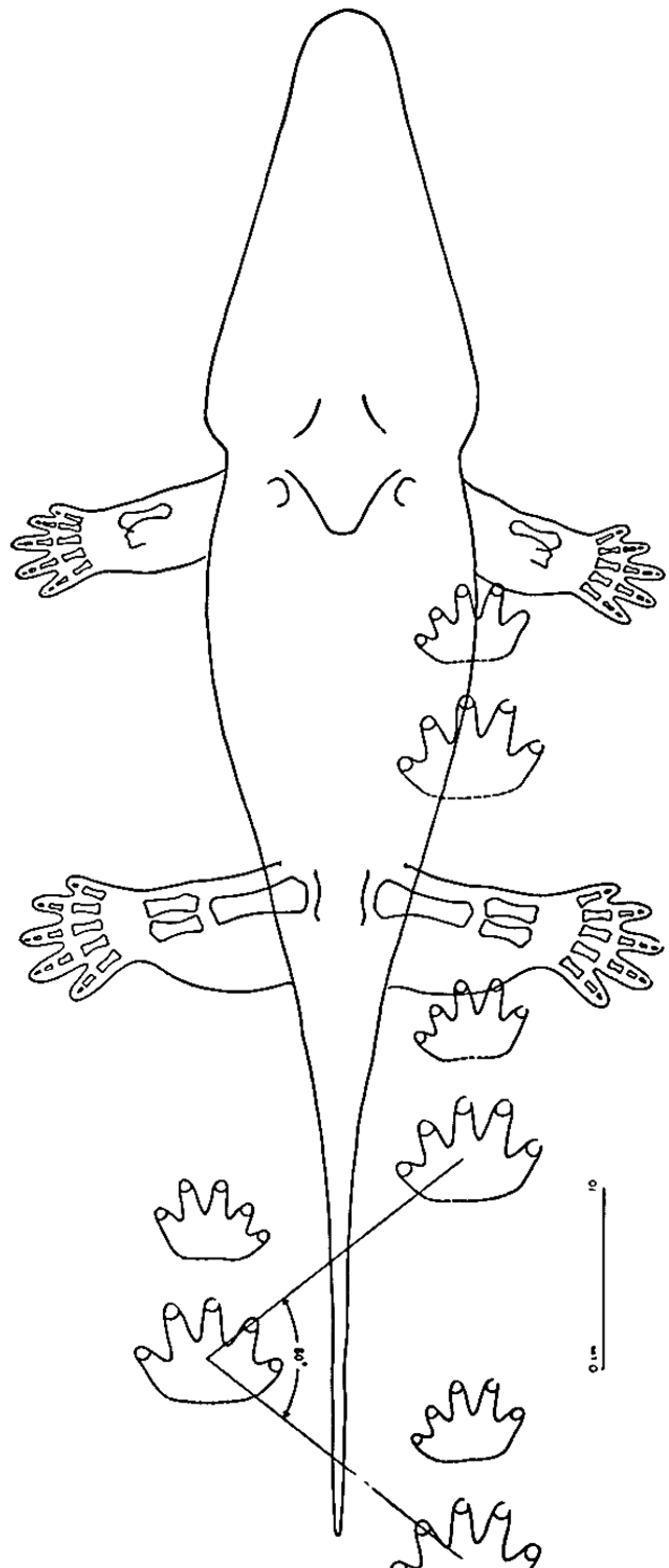

Fig. 10. Reconstructed outline of a capitosaurid from the Lower Moenkopi of Moqui Wash, with probable spacing and orientation of footprints in its trackway. Circle at digit tip indicates relation of digit tip impression to full impression of the foot. Outstretched limbs are not in the walking position.

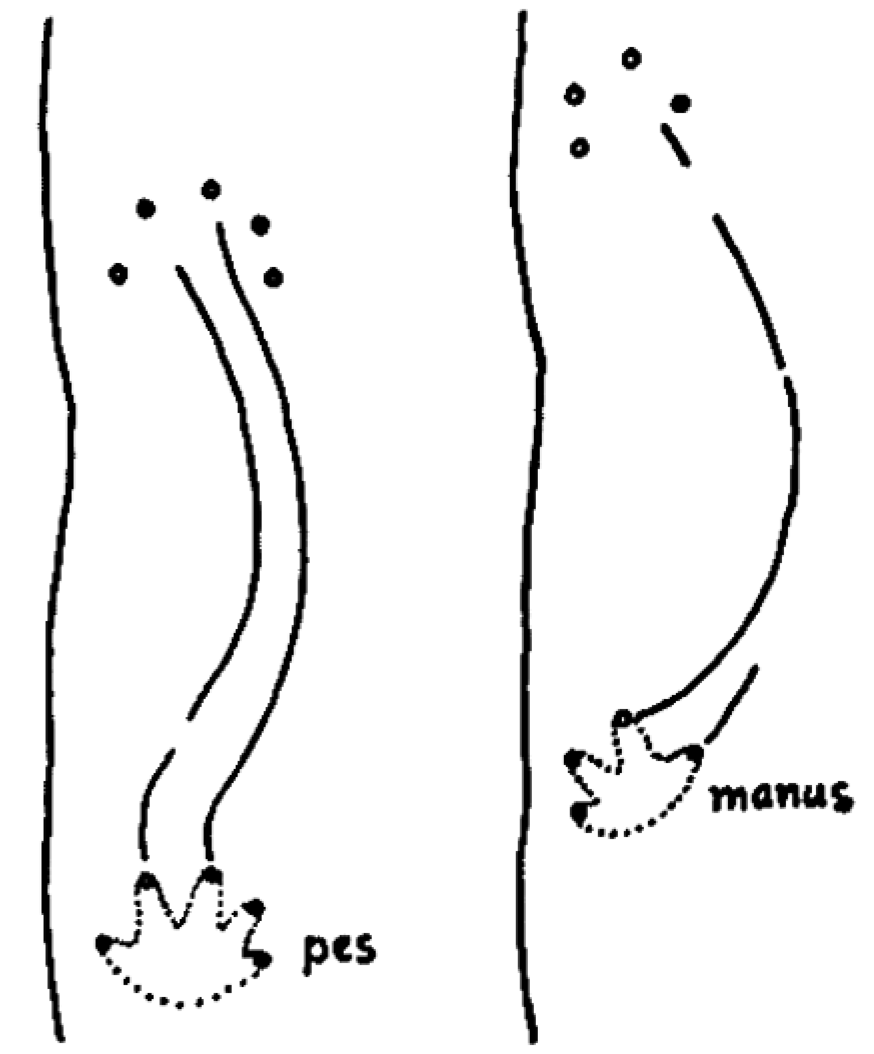

Fig. 11. Diagram of *Triturus* trackway made on smoked paper, showing relation of foot to digit-tip impression, also the extent and direction of toe dragmarks (manus and pes diagrammed separately for sake of clarity). × ½.

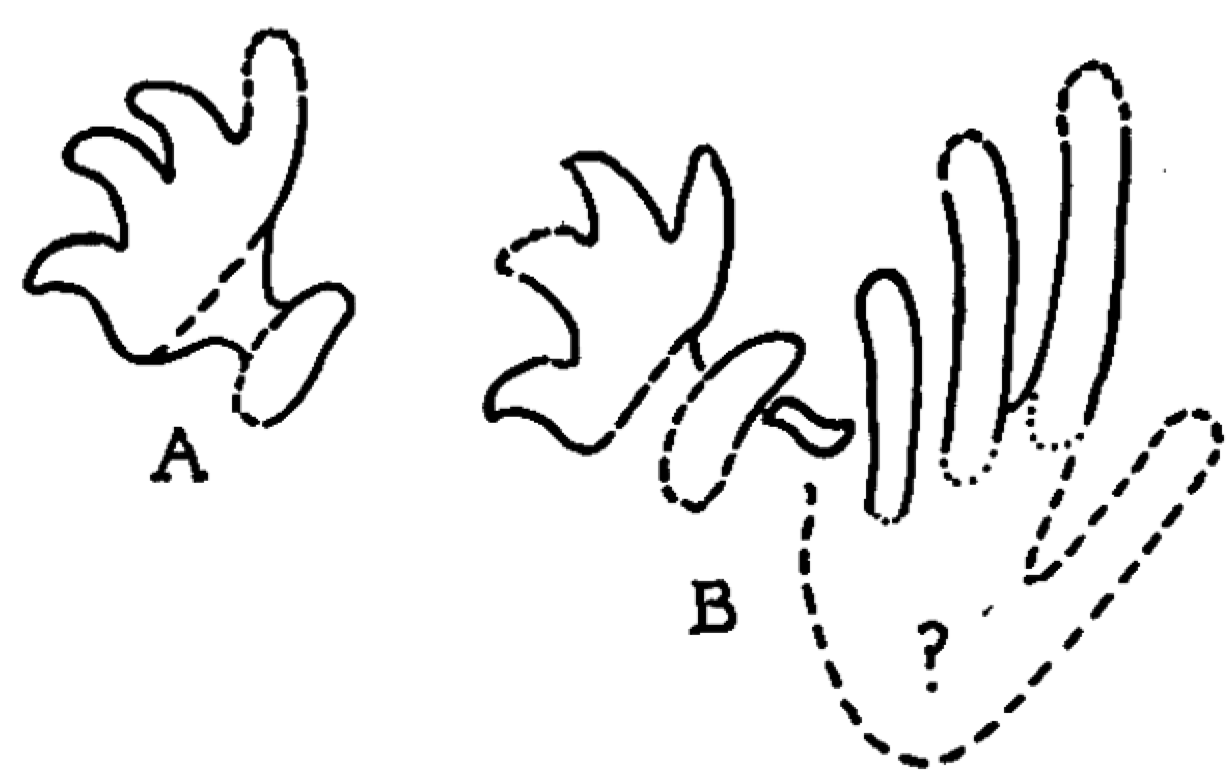

Fig. 12. Lacertoid footprints—Group 1, cf. *Akropus* Lilienstern: *A,* manus from trackway no. 37396 (pl. 29, no. 2); *B,* manus and pes from trackway no. 37343 (pl. 29, no. 1). × ½.

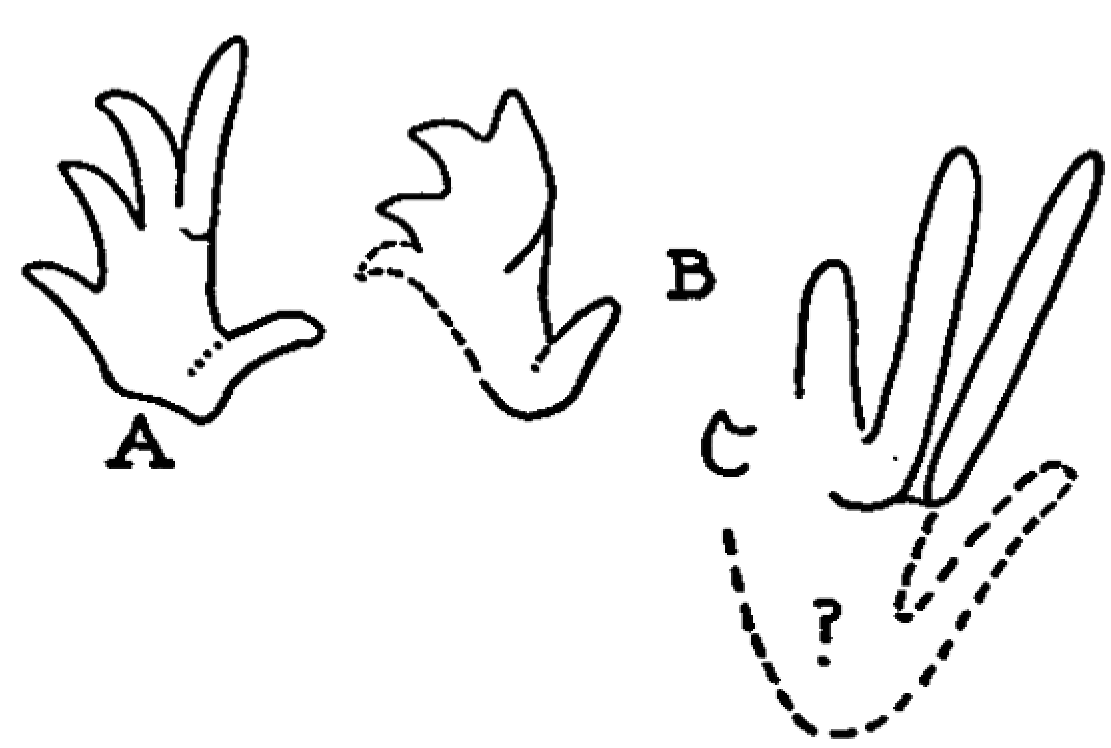

Fig. 13. Lacertoid footprints—Group 1, *Akropus* Lilienstern: *A,* isolated manus no. 37800; *B,* manus and pes from trackway no. 37797 (pl. 29, no. 3). × ½.

The length of free hind limb averages 59 per cent of the stride, 63 per cent if *Triturus* and *Ensatina* be excluded; the length of free hind limb is 67–75 per cent of the total width of the pattern of pes impressions; the pace angulation is 70–90 degrees. If 14 cm. be taken as the reconstructed free length of the capitosaur hind limb, the estimated average stride of the capitosaur trackway would be 22–24 cm., the average total width of the pattern would be 19–21 cm., and the pace angulation would remain the same because it is proportional and independent of size. If the conservative values are used, that is, 22 cm. stride, 21 cm. total width, and an even 80 degrees pace angulation, then the pattern of pes impressions can be laid out for the capitosaurid.

TABLE 2

MEASUREMENTS FROM SALAMANDER TRACKWAYS
(in centimeters)

Specimen	Hind limb (free length)	Average width of pes pattern	Average stride	Pace angulation (in degrees)
Salamandridae:				
Triturus rivularis	2.6	2.9	4.5	105
Ambystomidae:				
Ambystoma californiense	3.4	5.0	5.3	77
Dicamptodon ensatus	3.6	5.5	5.3	73
Plethodontidae:				
Ensatina eschscholtzii	2.1	2.5	4.1	105
Aneides lugubris	2.7	4.1	4.8	80

The combined length of the front and hind limb of the capitosaurid exceeds the glenoacetabular distance in the ratio of 10 to 8.5 ([gleno-acet.] 23 cm. ÷ [fore limb] 13 cm. + [hind limb] 14 cm. = .84 [cm.]). With salamanders as the criterion this would mean that in the walking gait the pes would emplace behind the manus about two thirds the distance between two consecutive manus impressions on the same side, that is to say, the trackway would consist of consecutive sets of manus and pes impressions, the manus occurring normally just anterior to the pes in the usual manner for tetrapods. The pes would never overlap the manus impression but would vary somewhat in position, anteroposteriorly, as a consequence of varying degrees of lateral undulation of the body. Both the manus and the pes impression would be approximately equidistant from the midline of the trackway and both would be oriented with the long axis (through digit III) more or less parallel to the midline. Walking salamanders point the foot forward and inward at least to this degree.

The tail of the capitosaurid is less than half the total length of the body while in salamanders it is usually more than half. The shorter the tail the less chance there is of a continuous tail mark appearing in the trackway. However, the long tail of a salamander does not always leave a clear trace and may even be carried free of the ground at times. Any lateral undulation of the body while walking is translated into a vigorous side-to-side movement of the short amphibian tail so that the terminal portion traces a sharply angulate pattern in

contrast to the straight or gently undulate tracing of a longer tail (*Triturus*, pl. 28, *A*). The capitosaurid tail seems too short to have left a continuous tracing and when on a sandy surface probably left nothing more than an occasional short erratic mark. Ordinarily the trackway of the animal would probably not show a tail mark.

Reconstructed Footprints

The cartilaginous carpus and tarsus and phalangeal joints of the capitosaurid indicate a supple foot which lacked a definite heel or posterior limit to the plantar surface. When the foot was rolled forward as a sort of supple termination of the limb, a method characteristic of salamanders, the result was a strong impression at the digit tip and a weak impression or none at all of the hind part of the foot. In salamanders the digit tip usually makes a ball-shaped impression which is more an expression of the type of locomotion than of the character of the digit tip itself. For example *Aneides* actually has expanded digit tips while *Triturus* lacks them, yet each trackway is characterized by ball-shaped impressions (pl. 28). *Triturus* depresses the digit tip possibly for better traction thereby obscuring the anatomical character in the impression.

The capitosaurid foot must have been somewhat similar to the much smaller one of *Triturus torosus*. The digits are flattened and have rounded but not swollen tips. Also, there is no evidence of any sort of digital or plantar pads. On a sandy surface, the foot probably left an arched series of rounded impressions which show no indication of details of the foot other than rounded and clawless digit tips. The footprint probably was similar to that made by the generalized foot of living salamanders of much smaller size. This is borne out by the type of footprint found in the Moenkopi formation.

Superposed on the basic arched series of impressions representing the capitosaur footprint would be the indication of fundamental characteristics of amphibian locomotion: outward rotation of the pes while implaced which results in elongation of the mark of the outer digits, particularly V; stronger impression of inner digits; presence of toe dragmarks. The toe dragmarks are common in salamander trackways and frequently lead unbroken from one footprint to the next. As such they clearly trace the path of the walking foot and thus furnish important facts about the locomotion. The salamander foot moves very close to the recording surface, closer as a rule than the *Triturus* used by Schaeffer (1941). This animal walked on glass; salamanders walking on unfamiliar surfaces often pick up the feet in an exaggerated manner. The trace of the digit, usually the central ones, indicates that the manus and pes describe paths of slightly different shape (fig. 11). Both manus and pes describe a lateral arc but the pes may describe a short, introductory, median arc before entering on the lateral one. As a result of this character, noticed principally in trackways of *Triturus*, the short toe dragmarks are slightly convex mediad as they leave the pes impression. Also, the marks originate from the median border of the digit tip impression. By contrast the manus describes a simple lateral arc more acute near the point of retraction. The toe dragmarks may originate from the lateral border of the digit tip impression.

The structure of the amphibian foot is such that conditions of the recording medium must be just right to result in a clearly impressed trackway. A large living ambystomid such as *Dicamptodon* may walk over a wet dune sand and leave not the slightest impression. The much larger size of the capitosaurid does not necessarily mean that it was more likely to record clear trackways. On thick lenses of river sand it would be possible for this large amphibian to move across the surface without leaving a recognizable trace. However, the amphibian type of locomotion often results in an arched series of rounded impressions on a recording medium which is too firm to take any other detail. A full impression of the capitosaurid foot in soft mud might have the outline indicated in the reconstruction.

Conclusion

There is little doubt that the footprints from the Lower Moenkopi are those of large amphibians and could not have been made by reptiles. Consideration of the important postcranial characters of the capitosaurid which occurs at the same level as the footprints and of its probable type of locomotion on land leads to the conclusion that amphibians of this kind could have made the fossil footprints. Furthermore, with the exception of a single long-snouted skull from Meteor Crater, which resembles the old world *Aphaneramma*, the Lower Moenkopi amphibia are capitosaurs. The size of the fossil footprints falls well within the range of size of the known capitosaurid amphibians from the Lower Moenkopi although they are too large to have been made by the animal represented by the articulated skeleton.

Environment

The geologic occurrence of labyrinthodont tracks and the skeleton of the capitosaurid provide several facts for further consideration. The skeleton was found in gently sloping foreset beds of a cross-bedded, ripple-marked sandstone of fluviatile origin. In this same sandstone a short distance to the south were found ripple-marked surfaces (positive) with many rounded impressions similar to those of the described footprints. It is impossible to distinguish a trackway among them. The surface may represent an exposed sandbar or sandspit upon which the capitosaurs crawled singly or in groups, moving about by sliding or walking so that a confusion of impressions resulted. The sandspits were adjacent to areas of sandy bottom which were rippled extensively by waves and currents of shallow waters. The firm sand was not conducive to impression of other than the tips of the digits.

I have observed a comparable record of this sort on a small tributary of the Russian River, California. On a small exposed sandspit beneath an overhanging bank were found many tracks showing where several newts, *Triturus rivularis*, emerged from the creek, and left a definite record of their presence. No trackway was recognizable because of the apparent aimlessness with which they moved over the surface.

The origin of the Moenkopi tracks under similar conditions may well explain why it is so difficult to find complete trackways, or indeed individual footprints.

The absence of reptile tracks from the sandspit surfaces and likewise the absence of amphibian tracks from the numerous well-preserved mudflat surfaces suggest that the stegocephalians lived in and around a river which afforded a quick retreat from a variety of reptiles prowling along the banks. An aquatic environment for the capitosaurid is independently suggested by the skin flap on the hind limb.

The sandstone ledge bearing the amphibian toe impressions has on its under surface the cast impression of an extensive mudflat which was traversed by reptiles of all sizes. The mudflat was probably along the shore or in an overflow basin until the main river channel shifted over it, thus bringing an abrupt change in living conditions. Hence the amphibian tracks, while occurring just above the reptile tracks, represent a later and different situation.

The Lower Moenkopi of Meteor Crater offers additional proof that labyrinthodonts lived in the same general vicinity as a variety of reptiles but in a different situation. The limestone which cast the extensive mudflat of the amphibian quarry contains remains of numerous capitosaurids, and of at least one long-snouted, fish-catching labyrinthodont. The bones could not have been transported very far, as indicated by lack of abrasion of delicate conical teeth of the amphibians.

LACERTOID TRACKWAYS (REPTILIA: ? PROTOROSAURIA) FROM THE UPPER MOENKOPI

Countless footprints of small reptiles are commonly associated with the trackways of *Chirotherium* in the Lower and Upper Moenkopi. The footprints may represent protorosaurs, primitive lizards, and rhynchocephalians, but for convenience are referred to as lacertoid, meaning lizard-like in body form. They may cover every available space on some mudflats, yet they provide an embarrassment of riches because the cluttered mass is generally unintelligible.

Occasionally one may find a surface containing a sparser distribution of footprints and be able to recognize consecutive steps of a trackway pattern. One such surface, a series of three slabs (pl. 29), was collected from the Upper Moenkopi several miles northwest of Cameron, between the Little Colorado River and Shadow Mountain (Mus. Pal. loc. V4208). The trackway surface is preserved on the underside of a thin sandstone lens. The rough surface adds to the difficulties of observation. It is the only trackway surface from the Moenkopi on which casts of salt crystals are associated with footprints.

Five short trackways representing at least two different reptiles of lacertoid form can be recognized. It was found necessary to coat the surface with water-soluble paint so that a photograph would show the pattern. Nonrelated, isolated footprints were painted over to lessen the confusion caused by poorness of impression and crisscrossing of patterns.

The five trackways seem to represent medium-sized individuals. Larger and smaller individuals are indicated by several isolated footprints on the surface, for example, the encircled manus (pl. 29). These trackways are the least satisfactory of all the Moenkopi material in clarity of impression; in part this is probably due to the lacertoid form of the reptile which made them (see below).

The trackways are generally characterized by a deeply impressed manus and a faintly impressed pes. At times a recognizable pes is missing. This condition is found in the trackways of recent lizards and is in sharp contrast with the trackways of *Rotodactylus* and *Chirotherium*. Thus the manus, and not the pes, is the stable element in the trackway. For this reason trackway measurements such as given in table 3 must treat the pes in relation to the manus, reversing the usual practice.

All five trackways exhibit a relatively wide pattern with pentadactyl footprints relatively distant from the midline. The pace angulation is low, below 90 degrees—100–120 degrees if figured from the manus pattern. The ratio of stride to pes length, estimated from incomplete impression, is about 5 to 1; that of manus length to stride is about 8 to 1.

The small manus is directed forward; the long-toed pes which occurs more or less directly lateral in position is turned out (position of longitudinal axis indicated in table 3).

The digits are slender and relatively longer in the pes. The character of the digit tip is usually obscured by poor impression, by distortion, or by both. Digits are slenderer in the clear, undistorted impression. The relative length and disposition of digits is generally similar to that found in recent iguanas and sphenodon. Manus digit V is divergent and recurved outward to a greater extent than in these recent forms; digits II–IV tend to curve strongly inward; the lateral border of metacarpus IV is partly free. The position of the metacarpal-phalangeal joint is generally indicated, particularly in digit IV.

Only the phalangeal parts of digits I–IV are recognizable in the pes. Presumably V was offset, leaving much of the border of the fourth metatarsal free as in recent lizards. The digits are generally straight.

The claws, if any, left little evidence of their presence although the digit tips seem more or less pointed. However, this may be equally true of trackways of some recent lizards (*Gerrhonotus*, *Sceloporus*) which have well-developed sharp claws.

No tail mark appears anywhere on the trackway surface.

The trackways can be differentiated easily into 2 groups: (1) Nos. 37343, 37796, 37797, 3 different animals of small size tending to show discontinuity between the impression of manus digits V and I–IV, suggestive of some chirotheriids, and a regularly impressed pes, I–IV. (2) Nos. 37344, 37795, a larger animal, probably the same individual, having a broad manus with strongly divergent V, regularly showing a fully impressed metacarpal region and a definite heel, and regularly lacking a recognizable pes impression. The stride is about 35 cm. compared to less than 30 cm. for group 1.

Group 1, cf. Akropus Lilienstern, 1939
(Figs. 12, 13)

Close analysis of the three trackways in group 1 is difficult because of the poor quality of the impressions. However, the two larger trackways (nos. 37796, 37343) are more similar to each other than to the third (no. 37797). They differ from each other as follows: in no. 37343 the pes is directly lateral to instead of

TABLE 3

Measurements of Fossil and Recent Lacertoid Trackways

Measurements	Group 2		Group 1			*Rhynchocephalichnus pisanus* Huene, 1941 (pl. VI, 4)	*Akropus* Lilienstern, 1939	*Sceloporus occidentalis*	*Gerrhonotus coeruleus*
	37795	37344	37796	37343	37797				
Pace angulation:									
Manus	118°	111°	97°–101°	100°–118°	109°–117°	117°–123°	......	132°	100°
Pes	......	78° [a]	79°	77°	85°	88°–95°	86° max.	90°	85°
Stride (in centimeters)	35	36.5	26	29.5	27	14	28	7.5	5
Ratio:									
Stride–pes length	......	(5 to 1)	(5.5 to 1)	......	......	......	......	3.5 to 1	4 to 1
Stride–manus length	8.5 to 1	8 to 1	7 to 1	8.5 to 1	8 to 1	6 to 1	......	6 to 1	6 to 1
Distance (in centimeters) from midline to:									
Manus	4–3	4.2	4	3.5–4	2.3	1.2	......	.5	.6
Pes	......	9	6.5–7	7	6	2.7	......	1.3	1.0
Longitudinal axis:									
Manus	IV	IV	III	III	IV	II–III	......	II–III	III
Pes	......	III	(II) [a]	II	II	I–II	......	I	II–III
Dimensions (length by width, in centimeters):									
Manus overall	4.5 x 4.3	4.7 x 4	3.8 x 3	3.5 x 3	3.5 x 2.5	2.4 x 1.6	......	1.3 x 1.2	.8 x .8
Pes overall	......	......	7x [a]	......	......	......	......	2.1 x 1.0	1.4 x 1.0
Pes I–IV	......	......	–x3.1	–x2.7	3.8 x 2.2	......	......	–x5	......

[a] Estimated

slightly behind the manus, so that the digit tips of manus digit IV and pes digit IV are even with each other transversely. The stride is more than 3 cm. longer. These differences could result from differences in speed of the same individual. Manus digit V does seem longer but the impressions are too poor to be

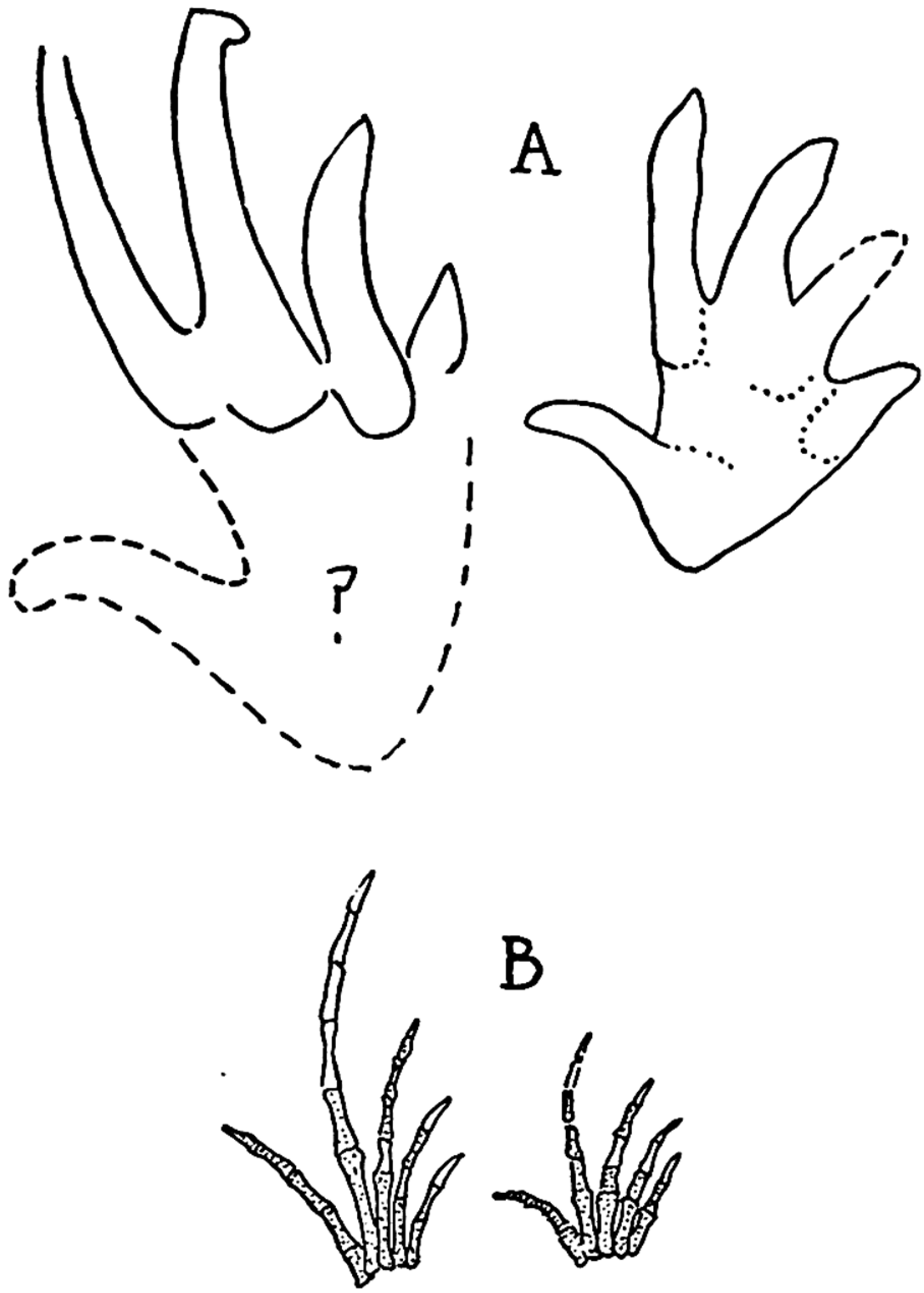

Fig. 14. *A*, lacertoid footprints—Group 2, manus and pes from trackway no. 37344 (pl. 29, no. 4); *B*, manus and pes of *Polysphenodon mülleri* Jkl. (after Huene 1941). × 1.

sure of the difference. For want of better material the two trackways must be considered as conspecific, probably similar individuals of one species.

The third trackway (no. 37797) is of a smaller animal with relatively longer, more slender feet yet with a stride nearly as long (27 cm.) as no. 37743 and longer than no. 37796. It probably represents a different species.

One isolated manus, relatively clear and undistorted in its impression (no. 37800), may represent an individual of the same kind as trackway no. 37797 but slightly larger. It shows the same interesting tendency for digit IV to be nearly straight or at least much less curved than digits I–III. A twisting of the

foot in the impression should tend to curve digit IV as much or more than III. Since this is not the case and since IV is parallel to the midline, the differential curvation may arise from a rapid gait in which the forward thrust of the manus tended to turn the ends of digits I–III which were not in line with the force.

Group 2, ? Rhynchocephalian
(Fig. 14)

Two trackways, nos. 37344, 37795, are so similar in pattern and impression that they could have been made by the same individual.

Identification of the manus impressions as such rests on a general similarity of pace angulation, orientation, and degree of impression with the manus patterns of group 1. Only in step 3 of trackway no. 37344 is there an impression

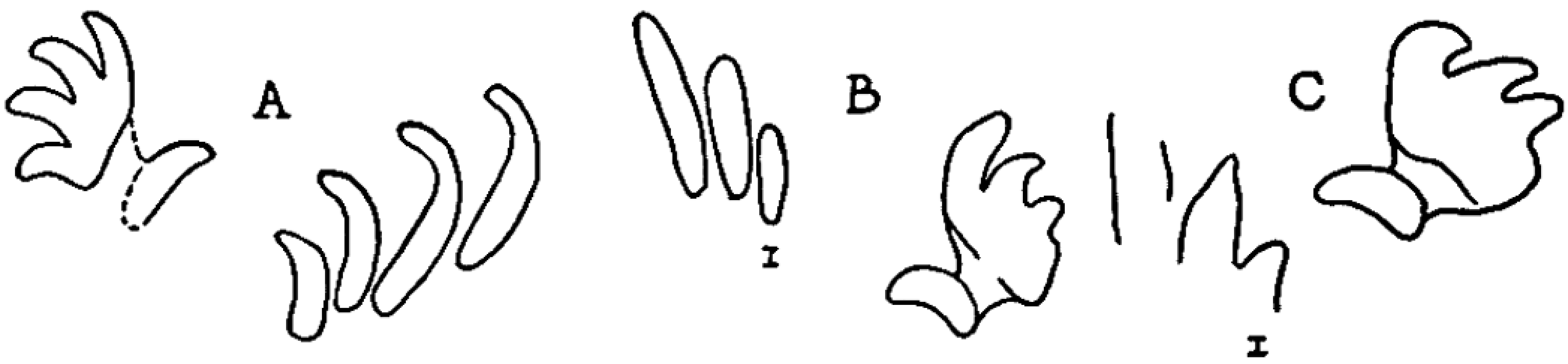

Fig. 15. Isolated sets of lacertoid manus and pes impressions from the Lower Moenkopi near Meteor Crater, loc. V4123: *A*, no. 37816; *B*, no. 37820; *C*, no. 37819. × ½.

that can be recognized as that of a pes. Tentatively it can be regarded as belonging to the trackway. It is oriented normally with respect to the manus and is the only one on the trackway surface which has definitely curved digits.

A trackway of a small recent lizard, *Sceloporus*, may show nearly undecipherable pes impressions regularly associated with deep and clear manus impressions. The relative size and structure of lizard feet seem to account for this. The generally lacertoid character of the fossil trackways suggests a similar explanation for the incomplete or missing pes in the fossil trackways.

The manus is more uniformly impressed and shows less distortion than in group 1. The digits are more widely spread and the metacarpal-phalangeal joint row is more nearly perpendicular to the longitudinal axis (through digit III). The metacarpal region is fully impressed and a heel with the apex at the base of digit V is regularly present. Also the line from the heel apex to the tip of digit I is nearly straight compared with the bulging outline shown by the only clearly impressed manus of group 1 (fig. 13, *A*).

The differences noted would indicate that groups 1 and 2 represent different genera, perhaps different families, of lacertoid reptiles.

Lacertoid Footprints from the Lower Moenkopi
(Fig. 15)

There is good evidence that reptiles of lacertoid form similar to those from Shadow Mountain existed in Lower Moenkopi time. North of Meteor Crater, and a quarter mile north of State Highway 66, several isolated sets of footprints were found impressed in fine-grained sandstone (Mus. Pal. loc. V4123).

The level is within 30 feet of the basal conglomerate of the Moenkopi, and is therefore at least as low stratigraphically as the Meteor Crater locality (V3835). No trackways were found, but the footprints are essentially similar to the Upper Moenkopi trackways.

Three of the clearest sets of footprints are shown. The manus of no. 37816 and no. 37820 is generally similar to that of trackways no. 37343 and no. 37796 from Shadow Mountain. The manus and pes of no. 37819 is of a stubby, thick-toed animal not represented in the Upper Moenkopi.

Relationships

In order to interpret the trackways I have obtained records from representative species of living lizards. Comparative material used here is much less abundant than desired but consists of several trackways of the small lizards *Sceloporus* and *Gerrhonotus*. Two pickled specimens (California Academy of Sciences) and a skeleton of *Sphenodon* and a skeleton of a large *Iguana* were also available.

The character of the trackways of groups 1 and 2 points definitely to an animal of lacertoid form. Among recent animals only tetrapod lizards and the rhynchocephalian, *Sphenodon*, make similar trackways. The similarity extends through details of pattern, attitude, relative position, and size of feet to general foot structure itself (see table 3). Certain of our recent lizards might record a nearly identical trackway. However, the lizard would have to be short-bodied to allow the pes to emplace lateral to the manus.[2] This is proved by a comparison of the trackways of the short-bodied *Sceloporus* and the long-bodied *Gerrhonotus* (pl. 42, *A* and *B*). Most lizards, including the large iguanas, fall in between these two extremes.

The general body form can be reasonably established as lacertoid, but it is difficult to assign the fossil trackways to a particular group of Triassic reptiles. The field can be fairly well narrowed down to lacertoid members of the Prolacertiformes (Camp, 1945), such as *Protorosaurus* and *Prolacerta*, and the Rhynchocephalia. The aberrant but primitive *Trilophosaurus* from the Upper Triassic of Texas can be eliminated as a possibility. Although lacertoid in form, the manus is very large relative to the pes and the animal itself is large (Gregory, 1944).

The trackways of group 1 are indistinguishable from those of *Akropus* described from the German Bunter by Lilienstern (1939). Essential details of footprints and trackway pattern are the same. The trackways of group 1 are likewise indistinguishable specifically from Chugwater Lower Triassic specimens described by Lull (1942) and by Branson (1946) from the vicinity of Lysite, Wyoming. Apparently neither Lull nor Branson had seen Lilienstern's 1939 paper. In my opinion the lacertoid trackways described separately by Lull as *Collettosaurus palmatus* and *Eurichnus jenseni* are congeneric as well as conspecific and should be referred to *Akropus*.

Lilienstern assigns *Akropus* to the Protorosauridae, in particular to *Protorosaurus*, a Permian reptile, while admitting strong rhynchocephalian affinities.

[2] It is known that the short-bodied lizards *Callisaurus* and *Uma* actually overstep the manus completely when running (Barbour, 1926; Stebbins, 1944).

The rhynchocephalians are excluded solely on the premise that their skeletal remains do not occur in the Lower Triassic. By contrast, Huene (1941) describes trackways very similar to *Akropus* from the Italian ? Keuper and calls them rhynchocephalian because skeletal remains of protorosaurs are unknown above the Lower Triassic. He states (1938) that this type of trackway is protorosauroid in the Bunter and rhynchocephaloid in the Keuper! In either event association with chirotheriid trackways is an interesting if not a significant fact. Ancestral lizards such as *Prolacerta* have not previously been considered as a possibility.

The trackways of group 2 differ from those of the Bunter and Keuper described by Lilienstern and Huene in the same manner as from group 1 in the Moenkopi, namely in the character of the broad manus. It is interesting to note that the manus fits the skeleton of *Polysphenodon* from the Keuper much better than *Rhynchocephalichnus* Huene except for size (fig. 14, *B*). *Polysphenodon mülleri* Jaekel is used to demonstrate the rhynchocephaloid character of the Italian Verrucano trackways of ? Keuper age (Huene, 1941). The trackways of group 2, as in group 1, indicate a short-bodied reptile commensurate with the body proportions of most rhynchocephalians.

Under the circumstances it seems best to admit that since a lacertoid form has been common to a great many unrelated reptiles in the past, the task of differentiating trackways of such animals may be impossible. A practical solution, if any, depends on a more thorough understanding of the trackways of living lacertoid reptiles as well as on the study of more and better fossil material. The only valid conclusion possible from the fossil trackways described here is that small to medium sized, short-bodied, lacertoid reptiles of several kinds and sizes were common during Moenkopi time. At least two of the trackways could have been made by rhynchocephalians.

Addendum

A Supposed Bipedal Trackway from Germany

A lacertoid trackway pattern consisting only of manus impressions and a tail mark is described (Huene, 1935) from the Triassic Stubensandstein of Germany as a bipedal pseudosuchian having a "striking resemblance to *Chirotherium*."

The pattern is similar in every way to lacertoid patterns of manus impressions and is much too wide for a bipedal trackway, having a pace angulation of only 100 degrees compared with the 150 degrees plus of a bipedal trackway. The proportions of the so-called pes are similar to the manus of group 2 except for smaller size, and certainly bear little resemblance to *Chirotherium*. The lack or apparent lack of pes impressions in a lacertoid trackway can be reasonably expected. Careful scrutiny of Huene's excellent photograph of the trackway surface in question shows obscure evidence of the "missing" pes in the expected position behind and outside the distorted right manus impressions in trackway "II."

The Stubensandstein trackways probably represent a heavy-headed lacertoid reptile possibly of rhynchocephalian affinities.

ROTODACTYLIDAE n. fam. (REPTILIA: PSEUDOSUCHIA)

Rotodactylus n. gen.

Definition.—Long-striding, sometimes semi-bipedal trackways of a small pentadactyl reptile. The manus is always closer to the midline and is always overstepped even in the walking gait by the much larger pes in a moderately narrow trackway pattern; pace angulation (pes) as high as 146 degrees in a running trackway and as low as 93 degrees in a walking trackway. The pes impression indicates a foot with an advanced digitigrade posture and with a strongly developed but slender digit V rotated to the rear where it functioned as a prop. Manus digit V may or may not be rotated backward but it has a propping function. Digit IV on both manus and pes is longer than III; digit I may fail to impress; claws are evident on digits I–IV. Scaly plantar surface, rarely shown, is characterized by transveresely elongate scales on the digit axis bordered by granular scales.

Type.—*Rotodactylus cursorius* n. sp.

Distribution.—Lower and Upper Moenkopi of Arizona, upper Moenkopi of southwestern Utah, a lateral distribution from Meteor Crater, Arizona, to Hurricane, Utah, a distance of 200 miles; possibly represented in the European Triassic.

Discussion

Footprints of a small reptile from the Upper Moenkopi of Cameron, Arizona, with digit V rotated to the rear have been described briefly and figured by Brady (1935). The reversed position of manus and pes—the manus being well behind the pes—was noted, but there was not enough material to establish the full trackway pattern. It was concluded that the footprints, left unnamed, were possibly those of a small primitive dinosaur which hopped aimlessly about.

Since the appearance of Brady's paper several trackways and isolated footprints of a somewhat smaller but similar reptile have been discovered in the Lower Moenkopi at Meteor Crater and near the top of the thick Moenkopi section near Hurricane, Utah. At Meteor Crater the trackways are associated with those of *Chirotherium* and all are preserved on the under side of a large series of sandstone slabs (figs. 16, 17). The trackways do not support Brady's conclusion but they do firmly establish the presence of a hitherto unknown group of reptiles in early Triassic time.

Trackways similar to *Rotodactylus* have not yet been described from the European Triassic. They may be represented there but are unrecognized because isolated poor impressions of the pes have a lacertoid resemblance. Certain footprints ascribed to rhynchosaurs from the English Keuper show a projecting spur at the back of the foot (Jeffs, 1894). Lilienstern (1939) is one of the first to study closely the small vertebrate tracks associated with *Chirotherium*. In his exhaustive description of a variety of small reptile tracks in the *Chirotherium* sandstone of Germany, he mentions nothing similar to *Rotodactylus*. The Cotylosauria, Chelonia, Protorosauria, and Pseudosuchia are represented there.

A small trackway somewhat resembling *Rotodactylus* except for the lack of a fifth digit impression is described as *Microsauropus clarki* by Moodie (1929) from redbeds assumed to be the Upper Clear Fork Permian of Texas. The trackway is assigned to the microsaurian Amphibia but this does not seem to

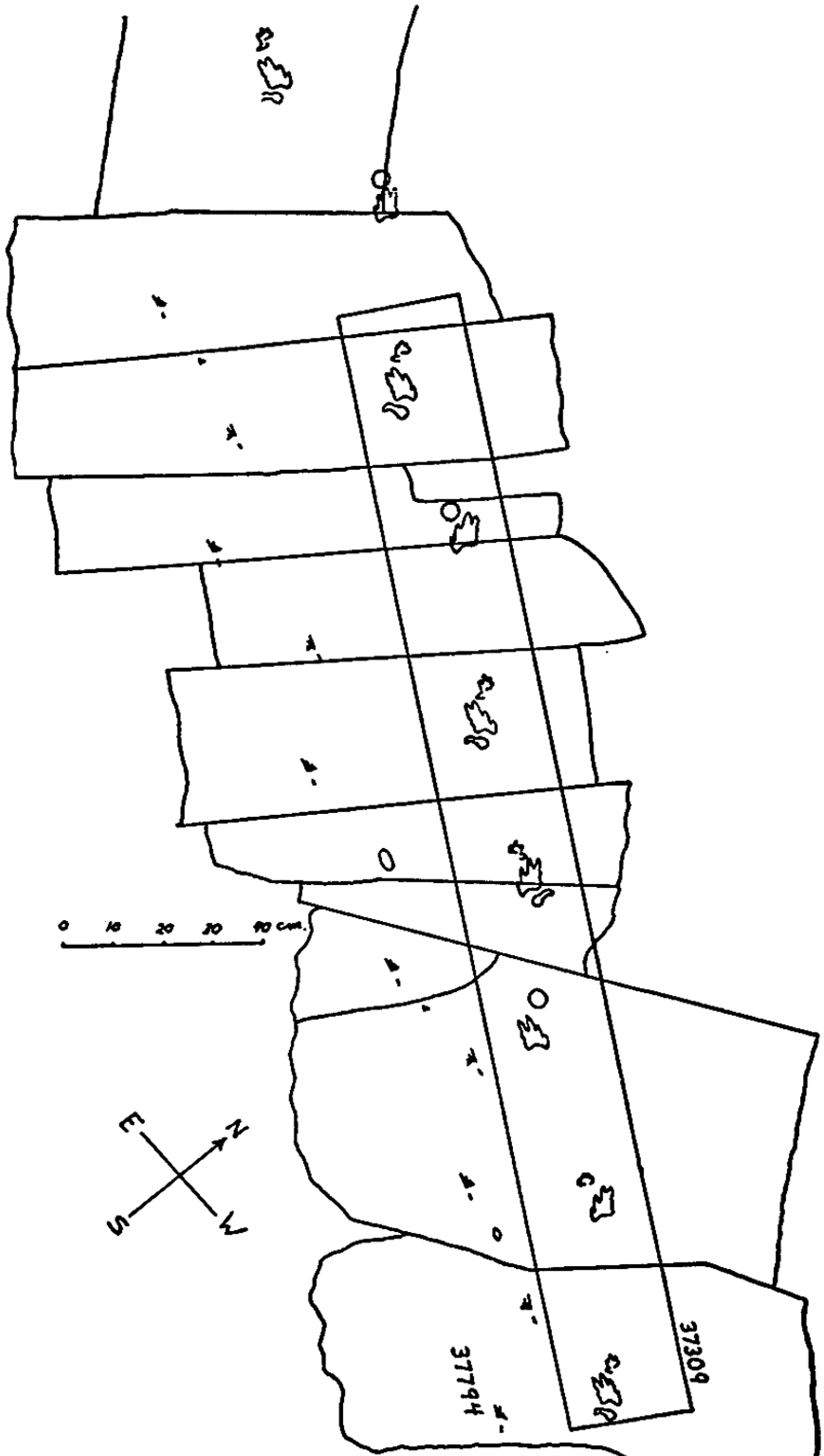

Fig. 16. Trackway diagram of *Rotodactylus cursorius* (type), associated with *Chirotherium minus* (in rectangle). Series of sandstone slabs from Lower Moenkopi, Meteor Crater loc. map at "a." Rectangular area shown in pl. 37.

be a correct designation. The pes clearly oversteps the manus completely in a relatively narrow, long-striding, trackway pattern. At least among living terrestrial salamanders, which are probably the most facile walkers of their class, this is impossible. Other particulars such as the large stride-pes length ratio may be used to prove a reptilian origin for *Microsauropus clarki.*

Rotodactylus cursorius n. sp.

Type.—Univ. Calif. Mus. Pal. no. 37794, trackway of 11 consecutive steps, fig. 16.

Referred specimens.—U.C.M.P. no. 37310, 4 consecutive steps; no. 37311, 4 consecutive steps; no. 37313, 3 consecutive steps; no. 37338, 2 consecutive steps.

Horizon and locality.—Lower Moenkopi near Meteor Crater, Arizona, U.C.M.P. loc. V3835, Meteor Crater loc. map at *a*.

Diagnosis.—Semi-bipedal, maximum stride 53 cm., maximum pes length 6 cm.; manus digit V turned backward, pes digit V often impressing distal half of its length; digits relatively slender with sharp claws on I–IV.

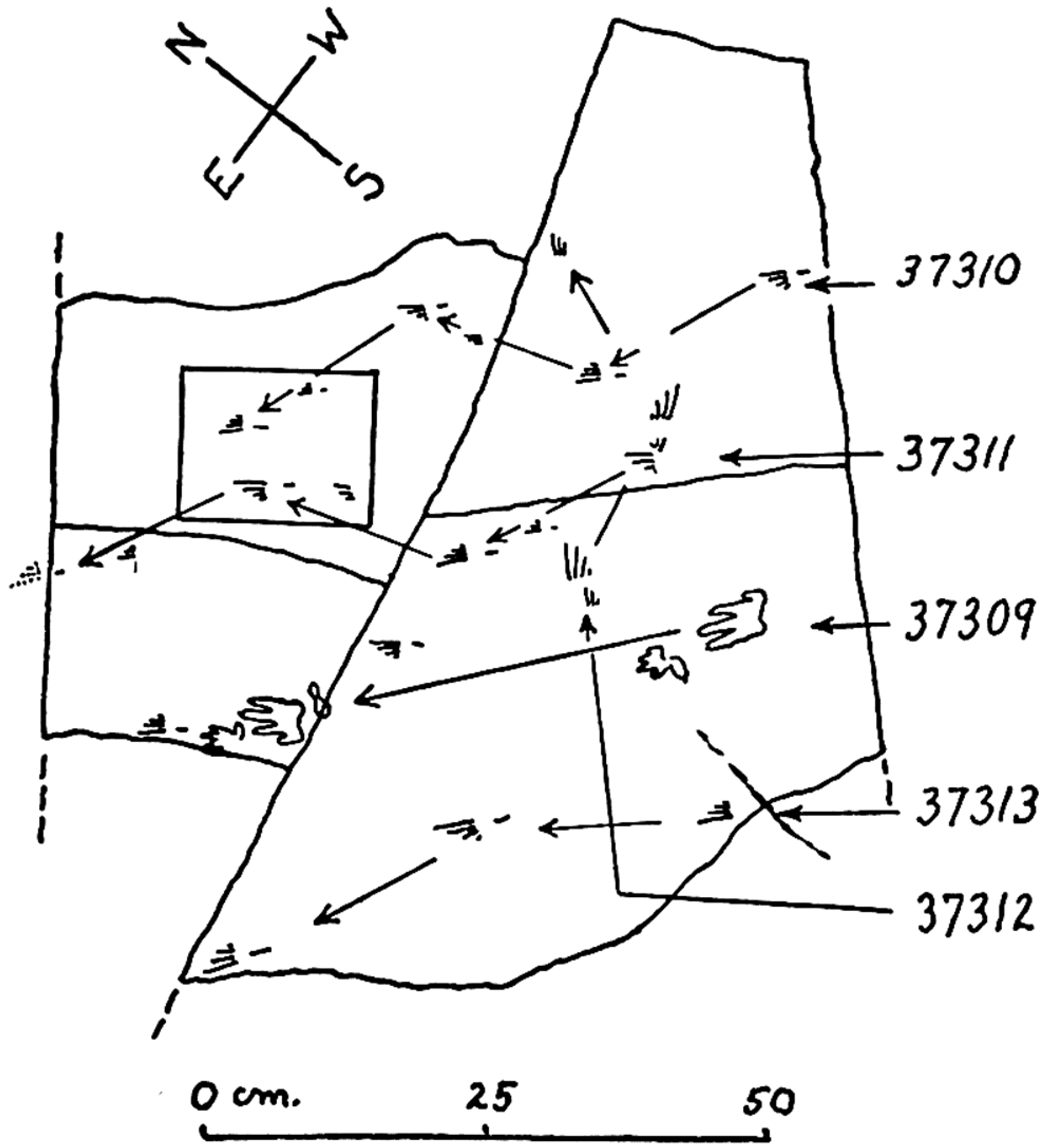

Fig. 17. Trackway diagram of *Rotodactylus cursorius*; rectangle shows area included in photograph of pl. 30, *A*. Footprints of *Chirotherium minus* (no. 37309) are continuation of trackway shown in fig. 16.

Occurrence

Trackways of *Rotodactylus* occur on an extensive mudflat surface at the base of a butte south of the amphibian quarry near Meteor Crater (loc. map at *a*). The mudflat surface was cast perfectly by a lens of sandstone from which a series of blocks was collected (figs. 16, 17). The character of the rotodactylid trackways indicates that the reptile which made them needed optimum conditions for clear impression. The mudflat was relatively smooth and untrampled but only soft enough locally to record the reptile clearly. Seemingly isolated footprints occur all over the large surface but only one long trackway, 11 con-

secutive steps (type), and 4 short ones can be identified. For reasons stated in the following description the trackways are considered to represent at least three different individuals of the same species. Variations in the trackway pattern are attributed to minor differences in gait. Comparative measurements are entered in the accompanying table together with those of *R. mckeei* and *R. bradyi* from the Upper Moenkopi.

It is impossible to recognize a full trackway pattern among the many rotodactylid footprints found in the amphibian quarry (fig. 21). They were poorly

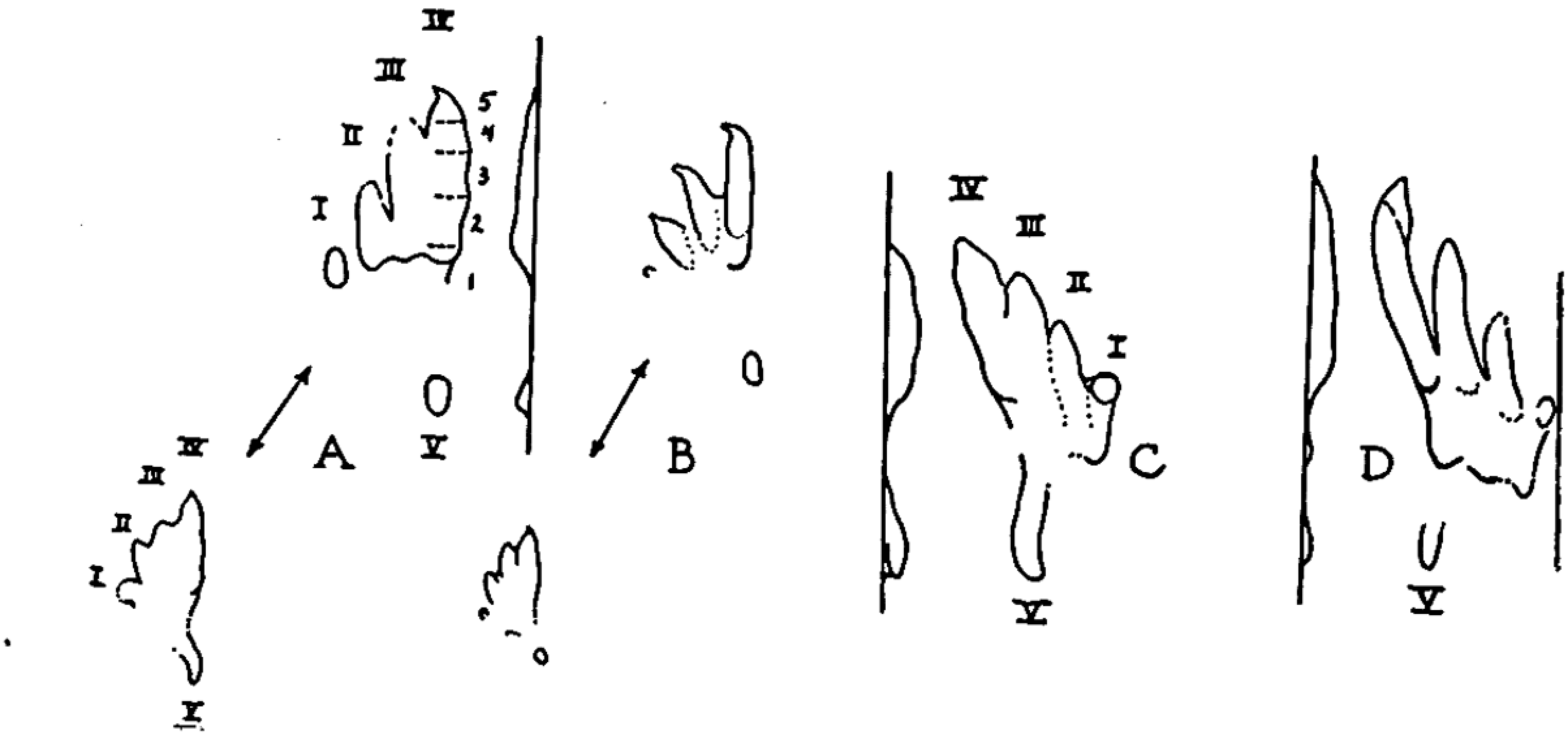

Fig. 18. *Rotodactylus cursorius: A,* no. 37211, manus and pes showing articular bulges in lateral outline of pes digit IV; *B,* no. 37310, manus and pes of small individual; *C,* no. 37794, pes deeply impressed and showing detail of proximal phalangeal area and of digit V; *D,* no. 37320, pes from amphibian quarry surface (fig. 21) also showing detail of proximal phalangeal area; lateral profile shown for pes in *A, C,* and *D.* × ½.

impressed in thin slippery marl and are poorly preserved by the overlying sandstone. They may represent a different species but the poor quality of the footprints prevents a description at this time.

Character of the foot

The character of the foot is fundamentally the same in all the footprints of *Rotodactylus* in spite of certain differences in the trackway pattern. Both manus and pes are readily distinguished from lacertoid and chirotheriid footprints in the backward rotation of digit V. The trackway pattern is also very different.

Pes.—The full impression shows the pes to be pentadactyl. Slender digits are progressively longer from I–IV as in the lacertoid foot but tend to be straighter except for a hook-shaped distortion at the claw tip. Short narrow claws are indicated on digits II–IV but not very clearly except on IV. Digit I impressed lightly if at all.

The foot apparently lacked any well-developed digital pads. The phalangeal formula is regularly indicated by knoblike swellings in the lateral border of digit IV only.

Several selected impressions (nos. 37320, 37335, among others) prove that the first phalanx of digits I–IV is elevated with the metatarsal and that the

functional surface of the digit begins proximally with the first phalangeal joint, not the metatarsal-phalangeal joint. Proof lies in the following facts: A few specimens (nos. 37335, 37320) indicate the position of the metatarsal-phalangeal joints by a row of faint impressions; the prone length of digit IV rather clearly indicates the presence of only 4 phalanges in the contour of the lateral border, which is one phalanx less than reasonable for such a long digit; the extreme shortness of the impression of digit I is best explained by the indicated structure.

The divarication of digits I–IV, as shown from deep impressions, is within 30 degrees. Digits II–IV tend to bunch together so that their individuality is obscure except at the tips. Digit V is rotated backward so that it makes an angle of about 160 degrees with the axis of IV. It extends backward relatively far, a distance roughly equal to the prone length of IV. The impression ranges from a round punch mark to an elongate facsimile of the distal length generally suggestive of a resilient rather than a stiff prop for the foot. A claw is not indicated even in deep impressions. The point of junction with the metatarsal region is never impressed—a further indication of the erect position of the metatarsal and first phalanx.

The fifth digit is well developed in length and width; in some specimens 1.5 cm. of free length is recognizable compared with 3 cm. length of functional surface of IV. It is plain that at least the distal half of the ventral surface was often in contact with the ground. When this was so, the overall length of the pes impression was increased since the more horizontal digit V was, the farther it extended backward. The full impression is gently arc-shaped, convex side out (fig. 18, *C*). It would seem that digit V was an important resilient prop at all times, most notably during the bipedal gait.

The phalangeal formula 2–3–4–5–3 is indicated by the relative length of the digits, especially since IV is proved to possess 5 phalanges. Digit V was relatively long so probably possessed at least three phalanges.

Manus.—The manus is usually impressed lightly, and digits I and V often fail to show. It is sometimes absent in one or two steps or it may be lacking altogether. It generally resembles the pes except in size and in the length of digit V. The metacarpals and first phalanges appear to have been more steeply inclined than the corresponding bones of the pes. The manus is relatively tiny, covering roughly one third the area of the pes. Digit V is relatively short but turned back in Lower Moenkopi *Rotodactylus.* Its position is usually indicated, if at all, by a round punch mark.

The skeletal structure of the manus is more difficult to interpret than the pes by reason of its tiny size and the semi-bipedal gait which controlled its impression. However, its general similarity to the pes suggests that the phalangeal formula was also 2–3–4–5–3.

The trackway pattern

No. 37794 (fig. 16, type trackway).—The trackway of 11 consecutive steps crosses the surface parallel to the trackway of *Chirotherium minus.* The individual footprints vary considerably in depth, the main reason being that the

TABLE 4

MEASUREMENTS OF ROTODACTYLUS TRACKWAYS

Measurements	*Rotodactylus cursorius*					? *Rotodactylus*	*R. mckeei*		*R. bradyi*
	37794 11 consecutive steps, semi-bipedal (type)	37310 4 consecutive steps, quadrupedal	37311 4 consecutive steps, quadrupedal	37313 3 consecutive steps, bipedal	37338 2 consecutive steps, semi-bipedal	37312 ?3 consecutive steps, quadrupedal, slow walk	38023 5+3 consecutive steps, quadrupedal (paratype)	38022 4 consecutive steps, quadrupedal slow walk	Brady specimen, quadrupedal
Stride (in centimeters)	53–46	35.5	39.5	50	(52)[a]	(29)	21.5	21.5	(62)
Pace (in centimeters)	....	....	....	....	26	14.5	....	....	31
Pace angulation:									
Pes	143°–131°	140°–142°	140°–137°	146°	(140°)	110°	119°–127°	93°	(125°)
Manus	....	172°	155°	....	....	....	150°–154°	137°–140°	....
Stride–pes length ratio	8.5 to 1	9 to 1	8 to 1	8 to 1	9.5 to 1	5 to 1	6.3 to 1	5.3 to 1	9 to 1
Manus length (in centimeters)	?	2.3	2.7	....	....	3.2	1.9	2.2	3.8
Pes length (in centimeters)	5.8	3.8–4.0	5.0	6.0	5.5	6.0	3.5	4.1	7.0
Pes from midline (in centimeters)	3.5	2.0[b]	2.0	2.4	(2.4)	4.5	1.0	2.5	6.5

[a] Figures in parentheses are estimated.
[b] Assuming digit I to be present.

animal stepped several times into open cracks. It follows that the uncertain footing may have caused the unevenness noted in the stride. In general the pes is deeply impressed with digit I, and the distal length of V showing clearly.

The stride is long relative to the pes length, 50 to 5.8 cm. or a ratio of 8.5 to 1, despite the fact that the rotated 5th digit makes the overall length of the pes about double that of a "propless" digitigrade pes. The pattern is fairly narrow, the pace angulation being 140 degrees, which is much higher than for lacertoids and lower than all chirotheriids except *Chirotherium diabloensis*. The relatively small size of the pes makes the pattern appear wider; this can be said also for the walking trackway of a placental mammal such as the wood rat, *Neotoma*, where the pace angulation is only 100 degrees. The pes averages 3 cm. from the midline and it points more or less directly forward, parallel to a line through the tip of digit IV and V. (Digit III points forward but it is usually obscure in *R. cursorius* so a nearly parallel line is substituted here.)

The pattern of relatively small manus impressions is the most informative element in the trackway. The manus occurs well behind the pes, almost halfway back to the preceding pes on the opposite side and nearly on a line between consecutive right and left (or left and right) pes impressions. Thus it is very close to the midline. As shown in figure 16, only the right manus made an impression. It is very faint in step 3 and missing in step 9. In none of the steps is the detailed character of the manus clearly shown. No special significance can be attached to the apparent lack of a left manus except that it may indicate an individual peculiarity or a favoring of an injured left manus. The sporadic absence of both right and left manus seems characteristic of *Rotodactylus cursorius*. a fact which strongly suggests that the pes carried most of the body weight in a semi-bipedal gait.

No. 37338 (not figured).—Two consecutive pes impressions are clearly shown on a sandstone slab from the same surface as the other trackways but not connected with the slabs shown in figs. 16, 17. The impressions are particularly clear and deeply incised, but no manus impression occurs between them. However, in front of the second pes a weakly impressed manus does occur in the expected position relative to a third consecutive pes not included on the slab. Here, then, is another sporadic occurrence of the manus. The estimated full trackway pattern is about the same as no. 37794 but the pes is turned out about 15 degrees from the midline.

No. 37313 (fig. 17).—The manus is lacking entirely in this short series of three consecutive steps; otherwise the trackway pattern is similar to no. 37794. In steps 2 and 3 the pes is deeply impressed, particularly in step 3, where much of the free length of rotated digit V can be seen. Apparently the overall length of the impression increased about .5 cm. as pressure on the foot flattened the arch formed by digit V and digit group I–IV. Digit I is clearly impressed in steps 2 and 3.

No. 37310 (fig. 17).—This short trackway is of similar proportions but smaller than no. 37794. The manus is lightly but clearly impressed on both sides of steps 2, 3, and 4 and its character can be recognized. It is toed-in slightly and nearly touches the midline.

The pes is only 3.8 cm. long compared to measurements of 5.0, 5.5, and 6.0 cm. for associated trackways and the digits are relatively slender. The trackway may represent a young individual. Additional trackways might show a constant difference in size and slenderness of digits, and thereby prove the existence of a different species; however, as noted in the description of several species of *Chirotherium*, noticeable variation in size is observed in otherwise similar trackways from the same surface.

No. 37311 (fig. 17).—This short trackway of 4 consecutive steps differs from nos. 37794 and 37310 in that the pes is turned out slightly (15 degrees) and the manus is closer behind the pes and farther from the midline. While the pes is nearly as long as that of trackway no. 37794, the stride is little longer than the much smaller trackway no. 37310. The differences in the pattern can reasonably be interpreted to be due to a somewhat slower gait.

The manus occurs on both sides of steps 2, 3, and 4 as in no. 37310. Also, as in no. 37310, the pes is not impressed deeply enough to clearly delineate digit I or to show more than the tip end of V. A relatively shallow pes impression seems to be correlated with the *regular* presence of the manus impression. But when the pes is deeply impressed the manus is sporadic in occurrence or missing entirely. This suggests a shift from a purely quadrupedal to a semi-bipedal gait.

No. 37312 (fig. 17).—The trackways previously described all seem to have been made by rapidly moving individuals, but there is one which appears to represent a slowly walking individual of *R. cursorius*. The trackway pattern is relatively wide, the stride short, and the manus occurs directly behind the pes at about the position of the spur mark. However, the impression of pes digit V is either lacking or obscured on the two available footprints thus giving the trackway a decided lacertoid appearance. This interpretation of the trackway gains considerable weight from newly discovered trackways of another species, *R. mckeei*, from the upper Moenkopi strata of southwestern Utah. It is of supplementary value to note that no lacertoid reptiles occur otherwise on the expansive trackway surfaces known from Meteor Crater.

Rotodactylus mckeei n. sp.

Type.—Univ. Calif. Mus. Pal. no. 38026, set of manus and pes impressions of large individual.

Paratype.—U.C.M.P. no. 38023, 3 and 5 consecutive steps of small individual.

Referred specimens.—U.C.M.P. no. 38022, 4 consecutive steps of medium small individual presumably made at a slow walk and showing excellent detail of scaly plantar surfaces of manus and pes; over 24 isolated manus and pes impressions occurring elsewhere on this trackway surface (no. 38021), some of which show excellent detail of the scaly plantar surface of the pes (nos. 38025, 38027) and of the manus (no. 38131).

Horizon and locality.—Uppermost Moenkopi beds exposed in a roadcut on State Highway 17, 9 miles west of Hurricane, Utah, U.C.M.P. loc. V4602.

Diagnosis.—Quadrupedal; maximum pes length 8 cm., maximum prone length of pes digit IV is 4.2 cm.; manus relatively narrow and long, with digit V set well back from the base of IV and directed obliquely forward; digits slender, claws narrow; plantar surface scaly, transversely elongate scales on axis of digit bordered by granular scales.

Discussion

The trackway surface exposed in the roadcut is cast on the underside of a thick siltstone which would be destroyed easily by weathering. The original impressions occur on the faintly ripple marked surface of a massive mudstone layer only slightly less coarse than the overlying siltstone. Very narrow cracks forming a polygonal pattern indicate a slight amount of desiccation. This combination seems to have resulted in exceptionally clear impression and equally clear preservation of the plantar detail of a reptile foot only 2.2 cm. long.

The many footprints of *Rotodactylus* which occur on this one surface immediately pose a problem discussed under *R. cursorius*. Does a small individual with a pes only 3.5 cm. long represent the same species as an otherwise similar individual with a pes over 6 cm. long, and are certain differences in the trackway pattern a result of differences in speed or in body proportions? For reasons stated below all the trackways and isolated footprints from the Hurricane surface are assigned to the single new species, *R. mckeei*. The specific name honors Mr. Edwin D. McKee, Professor of Geology at the University of Arizona, and Assistant Director of the Museum of Northern Arizona.

Two trackways can be clearly recognized. One, no. 38023, consists of 5 and 3 consecutive steps of a very small individual with a pes 3.5 cm. long. Detail of the manus and pes, including their position relative to each other, is the same as that of larger footprints for which there are no recognizable consecutive steps. The other trackway, no. 38022, consists of 4 consecutive steps of a slightly larger individual with a pes 4.1 cm. long which walked rather than ran over the surface so as to leave an exceptionally clear impression of the plantar surfaces and an exceptionally wide trackway pattern. Some of the large, presumably mature, individuals also recorded equally clear impressions of the plantar surfaces. The remaining footprints on the collected slabs belong to individuals of which the pes ranges from 5.7 to 8.0 cm. long. One of the isolated sets of manus and pes impressions, no. 38026, is designated as the type; the trackway of the smallest individual is designated as the paratype for want of a typical trackway of a larger individual.

No. 38026 (*type; pl. 32, A*).—The type at first glance appears very similar to *Rotodactylus cursorius;* the relative length and width of digits is the same, the over-all size is only slightly larger, and digit I of manus and pes barely brushed the surface, making a small rounded impression separate from that of digit group II–IV. The essential difference from *C. cursorius* lies in the relative narrowness of the manus and the character of its fifth digit. It has the shape of a miniature arcuate thumb and is directed forward and outward instead of backward. It is also set well back from the base of digit IV. By contrast, manus digit V of *R. bradyi* is relatively wider and set closer to the base of IV although it, too, is directed forward and outward. Less tangible differences are also noted: the posterior border of digit group I–IV of both manus and pes seems less well defined on the average than in *R. cursorius;* even in *R. bradyi*, where the pes is not deeply impressed, there is a more definite posterior border. The lateral border of digit IV does not show the articular bulges so clearly as *R.*

cursorius, and digit I of manus and pes and manus digit V are more often impressed, albeit lightly.

The type manus and pes measure 3.4 and 6.1 cm. long overall, respectively. A skid mark running back from the punch mark of pes digit V increases the length to 6.6 cm. maximum. There are other isolated pes impressions which are larger than the type; one is 7.5 cm., another 8.0 cm. long (maximum), and at least one isolated pes is 5.7 cm. At least some of this variation in length is probably due to variation in the inclined angle of pes digit V. Also there are isolated manus impressions which are slightly larger than the type, the largest being 3.6 cm. long, and some which are smaller, the smallest being only 2.7 cm. long. The important fact about this size gradation is that the still smaller individual represented by the paratype with a pes only 3.5 cm. long (no. 38023) can be reasonably regarded as the smallest individual of *R. mckeei*, not a different species. This contention gains support from the similarity of the plantar scalation of large and small individuals. A similar size range is noted in the description of *R. cursorius* and in the description of several species of *Chirotherium*.

No. 38023 (paratype, pls. 31, B; 32, B).—The paratype is a clearly impressed trackway of a small individual, manus and pes 1.9 and 3.5 cm. long, respectively, and is broken into two parts, one of 5 consecutive steps and one of 3. Typically, the detail of digits I–IV is blurred and digits II–IV impress as a group rather than individually. Digit I is lacking in all pes impressions except the second step of the series of three. The manus is definitely narrow and digit V is set well back and points forward and outward as in the type. Neither manus nor pes is impressed to the depth noted for *R. cursorius*.

The pace angulation is somewhat smaller than for *R. cursorius* being 122 degrees compared with 140 degrees. For the pattern of manus impressions the pace angulation is 152 degrees compared with two measured values of 172 and 155 degrees. The average stride is 21.5 cm. which makes the ratio of stride to pes length about 6 to 1, appreciably less than the 8 to 1 ratio of *R. cursorius*. Possibly associated with the lower pace angulation is the position of the manus, which is closer behind the pes than in *R. cursorius*. The tip of manus digit IV is usually about even with the punch mark of pes digit V. This relation holds for the isolated sets of manus and pes impressions occurring on the same surface. The manus is toed-in slightly, while the pes toes-out variably between 0 and 15 degress from a line through IV and V. There is no question but that the manus of the paratype is regularly present and evenly impressed and in this respect contrasts strongly with the sporadic presence and variable impression of the manus in *C. cursorius*. At the same time there is no evidence that the body weight shifted backward, causing the pes to impress deeply. It would seem that *R. mckeei* represents a purely quadrupedal rotodactylid.

No. 38022 (pls. 31, A; 32, F).—This trackway, consisting of 4 consecutive steps, is of an individual somewhat larger than the paratype, the manus and pes being 2.2 and 4.1 cm. long, respectively. The pes has been obscured in step 1 and lost except for the punch mark of digit V in step 3. Two characters of this trackway immediately strike the eye: the relatively wide trackway pattern with the manus well forward of its usual position almost as in lizards, and

the exquisite detail of the scaly plantar surface on the manus and pes. Such detail could only have been impressed by a slowly walking animal. The low pace angulation (93°), the turned-out pes (35°), the relatively short stride (21.5 cm.), and low ratio of stride to pes length (5.3 to 1) also point to a very slow walk. Were it not for the undoubted presence of the characteristic and unique spur mark of the fifth digit, this trackway might well have been called lacertoid.

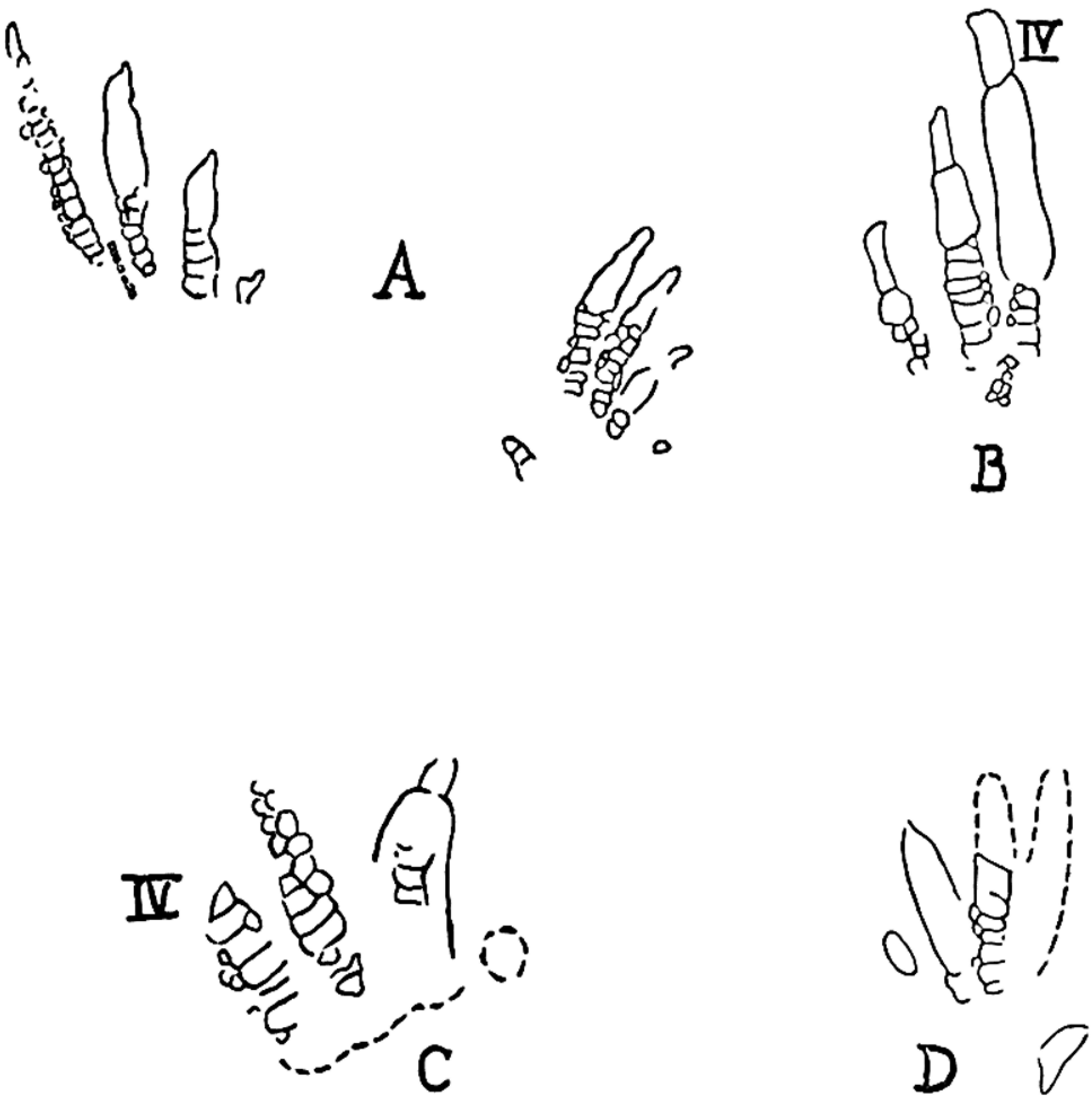

Fig. 19. Scaly plantar surface of *Rotodactylus mckeei*: *A*, manus and pes of trackway no. 38022 (pl. 31, *A*), slightly enlarged; *B*, isolated pes no. 38025, × 1; *C*, isolated manus no. 38131, × 1; *D*, isolated pes no. 38027, × 1½. *A*, *B*, *C*, and *D* shown in pl. 32, *F*, *D*, *E*, and *C*, respectively.

Long narrow claws, usually obscured in the running trackway, are clearly shown on digits I–IV. There is no clear indication of a claw on digit V of either manus or pes. Manus digit V, step 4, shows a scalation pattern nearly to the rounded tip of the impression, and pes digit V shows the usual rounded punch mark.

The scalation pattern of the plantar surface is shown to some degree in each footprint of the trackway. The pattern can be seen on manus digits II–V and on pes digits II–IV. It tends to be obscure on the distal part of the digit although pes IV of steps 2 and 4 shows it the full length. In step 2, pes digit IV shows faint prominences indicative of the position of phalanges 3, 4, and 5. The impressions are so delicate that extremely low-angle light directed from successively different directions is needed to work out full detail. Any one

photograph, therefore, cannot show maximum detail. Proximally the pattern disappears gradually, there being no readily defined posterior border.

The axis of each digit is characterized by a row of enlarged, usually transversely elongate scales more like the belly scales of snakes than plantar scales of any lizard or rhynchosaur. Distally on digit III of manus and pes the elongate scales seem to be replaced by smaller polygonal scales. This is true also for an isolated footprint (no. 38027) belonging to a large, presumably mature individual. The large axial scales are bordered by small granular or polygonal scales in alternate arrangement. The lateral and medial row of scales on pes digit IV (fig. 19, *A*) suggest the lateral and medial row of fringe scales of some modern lizards.

The scale pattern of this small individual of *R. mckeei* is essentially like that of the large individuals as proved by the fortunate occurrence of scalation detail on two large pes and one large manus occurring elsewhere on the same surface. This would seem to be strong proof in itself that the peculiarly wide-set trackway represents only a slow walking gait of a small individual of *R. mckeei*. It would also lend strength to the interpretation of the peculiarly wide-set trackway of *R. cursorius* (no. 37312, fig. 17) as that of a walking individual.

Rotodactylus bradyi n. sp.

Type.—Mus. Northern Arizona no. G2.2613A, a sandstone slab containing several footprints among which are two consecutive pes impressions with the manus impression associated with the second pes. This short trackway is designated as the type.

Referred specimens.—Footprints on slab no. G2.2613 other than those designated above; footprints on slab M.N.A. no. G2.2614 (pl. 30, *B*).

Horizon and locality.—Upper Moenkopi, probably the *Chirotherium barthi* zone, which is about 60 feet below the Moenkopi contact with the Shinarump formation, southwest of Cameron, Arizona.

Diagnosis.—Quadrupedal, stride 62 cm., maximum pes length 7 cm., maximum prone length of pes digit IV is 3.6 cm.; manus relatively broad, manus digit V turned forward with the tip close behind the base of IV; pes digit IV relatively short but still longer than III; digits thick, claws blunt.

The rotodactylid footprints described by Brady (1935) as those of a hopping reptile occur on the underside of two thin slabs of sandstone which were lent to me for study by Major L. F. Brady, curator of geology in the Museum of Northern Arizona. The specific name is given in his honor.

The limited area of Brady's slabs made it difficult to recognize the real trackway pattern which is essentially like that of *R. cursorius*. The long-striding pes oversteps the manus as much as 10 cm. (maximum separation). From the spacing of the only two consecutive pes impressions available, it is estimated that the stride is about 62 cm., the pace angulation is 125°, and the ratio of stride to pes length is 9 to 1. More complete material may alter these values somewhat.

Wherever the limited area permits, one can see that each pes is accompanied by an evenly and clearly impressed manus, unlike the condition in semi-bipedal *R. cursorius*. Yet the degree of overstep is similar and contrasts well with *R. mckeei*, in which the tip of the manus regularly occurs close behind the rotated pes digit V.

The foot of *R. bradyi* contrasts well with the other two species, especially in the following characters: the relative shortness of pes digit IV, the broad almost stubby manus with the forward-directed digit V set close to the base of IV, and the relatively wide digits with relatively heavy claws. The posterior border of digit group I–IV is sharply defined although the impressions are not particularly deep. The clearly impressed tip of manus digit V shows no sign of a claw, nor does the typical punch mark of pes digit V.

The reptile which made the footprints walked on a thin layer of mud probably overlying a firm sand base. Although the feet did not impress deeply, soft, thin mud was thrown up in perimetric ridges stronger on the side toward which the most pressure was exerted. Similar perimetric ridges can be observed in footprints obtained from recent mudflats where sedimentary conditions can be checked.

Relationships of *Rotodactylus*

The trackway of *Rotodactylus* can be assigned to the Reptilia on the characters evident in the footprints alone. Briefly, the advanced digitigrade posture of the foot and the scaly plantar surface exclude the Amphibia, the rotated fifth digit and the phalangeal formula exclude the Mammalia, and the presence of a manus excludes the Aves. A detailed survey of characters, factual and inferred, considerably restricts the number of reptilian types which could have made the trackways. Running trackways of *Rotodactylus cursorius* are the basis for statements unless otherwise indicated.

Successive sets of alternately right and left footprints, evenly spaced, indicate the usual alternate progression of limbs common to most tetrapods. There is no reason for supposing a highly specialized gait, such as characterizes certain placental mammals. The hopping gait suggested by Brady (1935) is shown to be a wrong interpretation occasioned by insufficient material. The characteristic position of the manus well behind the pes and much closer to the midline can only mean that a long hind leg consistently overstepped the fore limb by passing laterally; therefore, the torso must have been short. The alternate supposition that a set of impressions includes a pes and the next manus forward on the same side results in an impossibly long body for the animal in question.

The large degree of overstep and the relatively long stride would indicate a rapid gait in which all four feet were never touching the ground at the same instant. A slight degree of overstepping is shown in walking trackways of protorosaurs (Lilienstern, 1939) and of recent lizards such as *Sceloporus*. But the maximum degree of overstepping characteristic of *Rotodactylus* is not recorded by recent tetropods except those using a specialized gait such as the bounding gallop of cursorial mammals. The gridiron-tailed lizard, *Callisaurus* (Barbour, 1934, fig. 57) and the sand lizard, *Uma* (Stebbins, 1944), are known to overstep considerably when running rapidly but the fullness of impression shown by *Rotodactylus* could hardly be achieved by them. Even when *Rotodactylus* walked rather than ran, the pes still clearly overstepped the position of the manus as shown by occasional trackways of *R. cursorius* and *R. mckeei*.

The 50-cm. stride of *R. cursorius* is relatively longer than that of contempo-

raneous chirotheriids, about which there is little question of their dinosauroid form. *Chirotherium diabloensis*, with a slightly larger pes than *Rotodactylus*, has only a 25-cm. stride. The long striding *Chriotherium minus*, which parallels *Rotodactylus* in figure 16, has a pes about four times larger but a stride of only 75 cm., or one third larger. A lacertoid reptile with a larger pes than *R. cursorius* has only a 30-cm. stride.

Approaching the comparison of stride from another direction, we find that the ratio of stride to pes length is over 8 to 1 for *R. cursorius*, only about 6 to 1 for most chirotheriids except *Chirotherium minus* and *cameronensis* (8 to 1 maximum), and less than 5 to 1 for lacertoid reptiles.

The pes definitely bore most of the weight of the body, more than in a typical chirotheriid. Moreover, the manus is relatively smaller and sometimes failed to impress even though it may have been placed on the ground. Again the pes is more deeply impressed when the manus is occasionally or completely missing from the trackway pattern.

The forward-pointing foot had some lateral pressure exerted upon it, but not much, for the slender digits are nearly straight. The contour of the impression indicates that the foot moved straight forward from step to step with deviation in a vertical plane only. Considering the marked progression of length in digits I–IV, we have here a specialized use of a primitive pattern, a use which could conceivably initiate a shortening of digit IV, already accomplished by the earliest dinosaurs. The advanced digitigrade structure of the foot, in which the metapodials and first phalanges are elevated—as in some bipedal dinosaurs and cursorial birds such as the turkey,—in itself indicates an animal capable of rapid locomotion with limbs operating in a pendulum fashion.

In spite of the long stride and other evidence of a relatively rapid gait, the impression of the pes shows surprisingly little distortion. The pes was evidently emplaced and retracted at a steep angle with very little skidding or slipping apparent in the impression. One would reasonably expect that the proplike digit V would tend to slip forward, but the impression fails to show it. The seeming paradox actually demonstrates the essential character of the gait of *Rotodactylus*.

The lack of distortion in the print of pes V suggests that the digit touched the ground only during the "push-off," or as the maximum pressure was exerted, that is, as the center of balance moved over and forward of the foot. If we consider the character of the impression of digit V more closely, the explanation of the foot action becomes clear. As shown in figure 18, *C* (profile), the digit is actually forced backward in the impression. The punch-mark character of other impressions has already been mentioned. In other words, as the pressure on the pes (I–IV) reached a maximum, presumably when the center of balance moved over and forward of the foot, the pedal arch (V and I–IV) flattened, forcing V backward. Furthermore, the lack of any skid mark leading into the impression of V from behind indicates that the digit did not touch the ground until after the emplacement of digit group I–IV, and not until the pressure began to maximize and flatten the pedal arch; thus, an analysis of

the impression of pes digit V itself indicates that *Rotodactylus* was a long-legged animal which walked rapidly with a long springy stride, in great contrast with the plodding walk of the awkward-footed chirotheriids and with the sprawling gait of contemporaneous lacertoid reptiles.

Only one tail mark was found associated with *Rotodactylus* tracks. It is a narrow, keeled impression 7 cm. long, which runs parallel and in line with a linear series of manus and pes impressions of at least two individuals (amphibian quarry trackways, fig. 21, pl. 35, *A*). As already stated, I am not able to recognize a full trackway pattern here but the position of the tail mark is directly in line with the *Rotodactylus* tracks and at right angles to the nearest chirotheriid trackway. The tail mark substantiates what can be reasonably proved by the footprints alone; namely, that *Rotodactylus* possessed a long balancing tail in common with chirotheriids and bipedal dinosaurs.

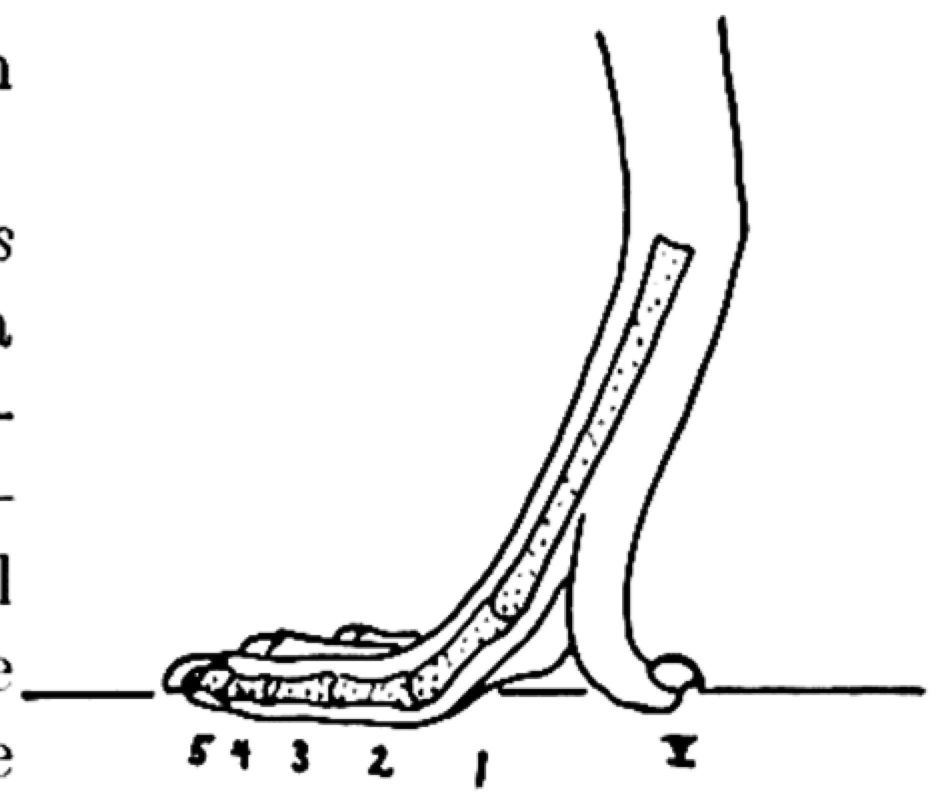

Fig. 20. Reconstructed pes of *Rotodactylus cursorius*. × ½.

The evidence from the trackways of *Rotodactylus* leads to but one conclusion. We are dealing with a cursorial reptile with a tendency toward bipedalism. The hind limbs carried most of the weight—at times in *R. cursorius* all of it,—and a long tail counterbalanced the prepelvic body mass. The body must have been slender and high off the ground, narrow through the shoulder regions, with the limbs long and well under the body, the knee and elbow pointed forward and backward, respectively. The fore limb must have been longer than in known bipedal dinosaurs in order to keep step with the hind limb, but the tiny size of the manus excludes any possibility of the fore limb's being as long as or subequal to the hind limb. Its functional length was possibly increased as in chirotheriids by more steeply inclined metacarpals.

The trackway of *Rotodactylus* cannot be associated with any skeletal remains from the Moenkopi as yet. Fragmentary skeletal remains from the Upper Moenkopi indicate the presence of large and small reptiles with pseudosuchian or coeluroid dinosaur affinities (Welles, 1947). More definite conclusions must await new discoveries.

The trackway of *Rotodactylus* is clearly that of an agile reptile of dinosaur-like form. The question arises whether the reptile may have been a primitive dinosaur or an advanced type of pseudosuchian such as the ornithosuchid, *Saltoposuchus*. The pes is more primitive than either group in having a long digit IV, but definitely dinosaur-like in the advanced digitigrade posture (elevated first phalanx). Pes digit V is reduced to a vestige in the earliest dinosaurs. It is more strongly developed in ornithosuchids, and has been reconstructed in *Saltoposuchus* by Huene (1921) as a forward-directed prop despite the fact that the phalanges of this digit are unknown in *Saltoposuchus*. As reconstructed by Huene, pes digit V would not be long enough to prop the foot after the manner of *Rotodactylus*.

In view of the probable diversity of dinosaurian ancestral lines it is possible

that the *Rotodactylus* foot could have been prototypic of some known type of dinosaur. The Upper Moenkopi species, *R. bradyi* has a shortened pes digit IV. In all species pes digit V may have lost its function and subsequently its strong development, and digit IV may eventually have become shorter than III in theoretical descendants of *Rotodactylus*. The foot structure then would be much closer to that of early dinosaurs.

Possibly the three-toed dinosaur type of foot was already developed in Bunter and Keuper time, and was a contemporary of the chirotheriid and rotodactylid foot. A three-toed "dinosaur" track is described from the Italian ? Keuper in association with *Chirotherium* (Huene, 1941), and dinosaur tracks are reported to occur in the German Bunter (Soergel, 1925, p. 88).

The trackways of *Rotodactylus* suggest an affinity with some branch of the Pseudosuchia, encompassing reptiles of dinosaur-like form with relatively long, slender fore limbs as compared with purely bipedal dinosaurs. The foot structure is unique and perhaps is prototypic for the specialized running foot so successful among dinosaurs and birds (see also p. 411). At least it demonstrates one method by which the reptilian foot may have gained a cursorial posture.

CHIROTHERIIDAE ABEL, 1935 (PSEUDOSUCHIA)

Definition.—Relatively narrow, quadrupedal trackways indicating the normal tetrapod walking gait; in the walking gait a small pentadactyl manus impression regularly occurs immediately in front of, but never overlapped by a much larger, pentadactyl pes which generally resembles a reversed human hand. Manus and pes are digitigrade, and in large forms the pes tends to be plantigrade; digits I–IV point more or less forward, manus digit IV is always shorter than III, digit V is divergent and well developed as a crude prop for the foot; strong claws are indicated on digits I–IV, infrequently on V of manus and pes, claw on III being largest; the footprints may or may not show specialized metatarsal and phalangeal pads. Clear impressions often show a granular or beaded skin surface.

Reptiles represented by trackways probably dinosaur-like in form, and in body proportions showed arrested tendency toward bipedalism. In smallest species pes only 3 cm. long; in largest species pes exceeded 30 cm.

Type genus.—*Chirotherium* Kaup, 1835.

Distribution.—Family Chirotheriidae flourished at time of redbed formation in early Triassic time. Well represented in North America in Lower and Upper Moenkopi of Little Colorado River region by total of eight species. *Chirotherium* occurs as far east as Snowflake, Arizona, and as far west as Rockville, Utah, a lateral distribution of 250 miles. Sparingly represented in Europe in Middle Bunter and well represented in Upper Bunter and Middle Keuper. In Upper Triassic Newark Series of Eastern North America one poorly recorded trackway indicates last appearance of family. Competition with increasing numbers of dinosaurs possible contributing factor to final extinction of the family.

GENUS CHIROTHERIUM KAUP, 1835

Chirosaurus Lydekker, 1890.

Saurichnites Kirchner, 1927.

HISTORY OF CHIROTHERIUM

The history of the discovery and description of the handlike footprints from the Triassic known as *Chirotherium* is both interesting and devious. Bernhardi (1834) described but did not name the first trackways of *Chirotherium* from the Bunter Triassic of Hessberg near Hildburghausen, Germany. He re-

marked on the similarity of the impressions to the human hand and thanked Mr. C. Barth for bringing the tracks to scientific attention. Several weeks after the appearance of Bernhardi's letter in the *Neues Jahrbuch* Sickler independently published his letter to Blumenbach (Winkler, 1886), in which *Chirotherium* tracks were described more fully but still left unnamed. A year later in the *Neues Jahrbuch* (1835) the letter was published with added observations

TABLE 5

STRATIGRAPHIC OCCURRENCE AND SYNOPSIS OF SPECIES FROM THE MOENKOPI

Species	Occurrence	Pace angulation	Stride-pes length ratio	Relative body size	Range of pes length (in centimeters)	Relative length of pes digits
C. diabloensis . . .	Lower	140° (160° running)	5 (7 running)	1	3.5–5.3	III and IV equal, V long
C. cameronensis.	Upper	160°	8.5	1	5	III and IV equal, V short
C. minus.	Lower	160°	8.5	2	8.5–12.2	III longest, IV subequal
C. barthi.	Upper	170°	5	3	13.5–24	III longest, IV and II subequal
C. moquiensis. . . .	? Upper Lower	. . . .	5	4	30	IV subequal to II
C. rex.	Upper ? Lower	. . . .	. . . .	4	33	IV subequal to II
C. coltoni.	Lower	. . . .	. . . .	2	12.2	IV much shorter than II
C. marshalli.	Upper	170°+	5	3	22	IV much shorter than II

by Bronn (1835). Sickler is credited, probably wrongly, with the first description of *Chirotherium* (Winkler, 1886). Later, Kaup (1835) formally designated the Hildburghausen tracks described in Sickler's letter as "*Chirotherium barthii*" with the alternate generic name, *Chirosaurus*, to be used in the event the animal proved to be reptilian. This would now be considered an irregular procedure taxonomically. Much later, when Lydekker (1890) changed *Chirotherium* to the more appropriate *Chirosaurus*, few workers followed him. Soon after Kaup's paper, Sickler (1836) described two different groups of *Chirotherium* tracks from Hildburghausen, naming the smaller *C. minus*, and the larger *C. majus*. The latter subsequently proved to be synonymous with *C. barthi*.

Chirotherium tracks had been noticed somewhat earlier in England than in Germany but it was not until 1838 that a committee report of the Natural History Society of Liverpool was presented before the Geological Society in London (Cunningham, 1839) describing footprints from the Keuper of Storeton. Much later, Morton (1873) formally designated the pes and manus described by Cunningham as *Chirotherium storetonense*. Also at the 1838 meeting, Egerton (1839) described two gigantic pes impressions 15 inches long as *C.*

herculis. Nearly forty years later Hornstein (1876) described the next species of *Chirotherium*, *C. geinitzi*, from the German Bunter. It was considered synonymous with *C. barthi* by Lydekker (1890) and is here considered a genus indeterminate.

In 1886 Winkler included in his *Histoire de l'Ichnologie* a timely compilation in French of all the important papers dealing with tracks and trackways written between 1834 and 1886.

It was after the turn of the century that another kind of *Chirotherium* was described, but left unnamed by Beasley (1906, 1907) and Lomas (1907). This is the curious chirotheriid with a small manus from the Storeton Keuper of England, mistakenly called *Chirotherium storetonense* by Soergel (see p. 345).

The interest in *Chirotherium* tracks spread to the United States where King (1844) and Moore (1873) described supposed chirotheriid tracks from the Carboniferous of Pennsylvania. These are not *Chirotherium*. Hitchcock (1898) finally found real evidence of the genus in the Upper Triassic Newark series of Eastern North America.

In 1917 Willruth wrote on *Chirotherium*. His paper is mainly notable for bringing to light an unpublished manuscript of 1889 by J. G. Bornemann who had made a study of *Chirotherium* tracks in Germany. He seems to have been one of the first to emphasize the importance of the trackway over isolated footprints. Willruth published Bornemann's original drawing showing part of six *Chirotherium* trackways on a series of sandstone slabs. In the manuscript, Bornemann described as *C. gallicum* (photo by Willruth, pl. III) a particularly clear pes of *C. barthi* which shows the character of the skin surface. Bornemann also discussed *C. majus* (= *C. barthi*) and *C. minus* previously described by Sickler. Possibly as a posthumous award for Bornemann's unpublished work Willruth saw fit to rename *C. minus*, calling it *C. bornemanni*.

The appearance in 1925 of Soergel's paleobiological study of *Chirotherium* is an important event in the history of trackway studies. From the taxonomist's point of view it is unfortunate that Soergel published the paleobiological treatise prior to the appearance of the formal description of chirotheriid species discussed in the treatise. So far as can be determined the "grössere Arbeit" promised in 1925 has never been published. As a result the validity of several new species of chirotheriids rests on photographs and casual reference. On the basis of Soergel's work, Abel (1935) proposed the new family, Chirotheriidae.

Later publications by Lilienstern (1938, 1939) and Huene (1941) have added new species of chirotheriids to the records but it still remains for someone to review thoroughly the chirotheriid fauna of Europe.

The later history of *Chirotherium* in North America is brief. In 1935, L. F. Brady described two consecutive steps of a large chirotheriid from the Moenkopi of Arizona and concluded that they resembled *C. barthi* of Europe. Interest generated by this new occurrence ultimately resulted in the study presented here.

Most of the history of *Chirotherium* revolves about the problem of determining the kind of animal which made the trackways rather than about the problems of specific determination. Soon after the first trackways were de-

scribed by Bernhardi additional trackways were discovered both in Germany and in England. A hot debate commenced at once concerning the origin of the handlike tracks. The striking resemblance of the pes impression to the human hand was extremely confusing. No two authors could agree that the "thumb" represented digit I or V. Egerton (1839) even used a novel system of designation in which digit V is called the "thumb" but IV is called "toe 1," III "toe 2," etc. Giant apes, mandrills, marsupials, primitive dinosaurs, and labyrinthodont amphibians were at different times suggested as the animals responsible for the trackways. The extremes were suggested early so that the following 100 years saw a narrowing of possibilities.

In 1841 Owen suggested the heavy-headed labyrinthodont Amphibia as the originator of *Chirotherium* tracks. This view took precedence over less authoritative but more correct views and culminated in 1855 with Lyell's impossible picture of a froglike labyrinthodont (*Chirotherium*) walking cross-legged.

Various workers became more and more convinced that some sort of reptile had made the trackways of *Chirotherium*. Eventually Watson (1914) satisfactorily narrowed the possibilities to some type of dinosaur possibly ancestral to *Plateosaurus*. Watson's short but able approach to the problem foreshadowed the later paleobiological work of Soergel, but apparently could not offset the old association of *Chirotherium* with the labyrinthodont Amphibia. Watson noted particularly the relative narrowness of the trackways and the possible indications of the pedal skeleton shown by the footprints, and correctly designated the recurved "thumb" of the pes as digit V.

In 1917 Willruth concluded that the controversial fifth digit of both manus and pes was a fleshy appendage without skeletal parts. Willruth had not seen Owen's paper but he realized that the gait of *Chirotherium* consisted of a nattural alternating pace. He could not, however, admit that the fifth digit could possibly be so large. Here we see the expression of an idea that had persisted ever since the pes of *Chirotherium* was first likened to a human hand. It was the attempt to keep the small "little finger" on the outside and the large "thumb" on the inside, as in the human hand, that led to Lyell's cross-legged batrachian. Willruth's teacher, J. Walther (1917), followed his student in championing the fleshy-appendage theory but no one else seems to have taken the theory seriously. Isolated horseshoe-shaped tracks attributed to the fleshy appendage by Willruth and Walther appear to be identical with the "current indicators" described from the Arizona Moenkopi strata.

In 1925 the paleobiological work of Soergel appeared. Many different specimens of *Chirotherium* from England and Germany were closely studied in order to determine the approximate body proportions and gait of the animals which made the trackways. The many excellent trackways of *Chirotherium barthi* form the principal basis of Soergel's conclusions. Impressions of the skin, claws and indications of the number and character of the phalanges and metapodials were of critical importance. A clear differentiation of species is not made in this paleobiological study. Soergel found that the probable skeleton of the pes of *C. barthi* compares most closely with the pes of *Euparkeria capensis*, an ornithosuchid pseudosuchian.

Soergel's reconstruction of the anatomy of the typical species, *C. barthi*, and his allocation of chirotheriid trackways to the dinosaur-like pseudosuchians have met general acceptance. The latest edition of Zittel's *Textbook of Paleontology* (1932) follows Soergel and, in addition, places *Chirotherium* in the family Ornithosuchidae. Abel (1935) defines the genus according to the work of Soergel and places it in a separate family of the Pseudosuchia, the Chirotheriidae. Since the work of Soergel, the most noteworthy attempt to relate *Chirotherium* to actual skeletal remains has been made by Huene (1936). The complete skeleton of a stagonolepid pseudosuchian, *Prestosuchus chiniquensis*, is reconstructed and the conclusion made that while it does not exactly fit *Chirotherium*, the two are close and both belong to the Stagonolepidae. The view is taken in the present study that while *Prestosuchus* may be closer to *Chirotherium* than anything previously known, there are enough important differences between the two to warrant the continuation of Abel's Chirotheriidae as a distinct family of the Pseudosuchia.

PREVIOUSLY DESCRIBED SPECIES

A systematic review of species of *Chirotherium* cannot be considered complete unless the original specimens are inspected by the reviewer. However, it is worth while to assemble here what information is available; most of it comes from European publications, some of which are little known and are not ordinarily at the disposal of North American workers.

Chirotherium barthi Kaup

This species is discussed in detail on page 364, below.

Chirotherium minus Sickler

This species is discussed in detail on page 358, below.

Chirotherium herculis Egerton, 1839

Chirotherium barthi var. *herculis* Lilienstern, 1939.

The species is described from two giant footprints 15 inches long from the English Keuper at Torperley (Cheshire) "in the upper part of the new red system." The description is deficient but the footprints represent a valid species and not a variety of *C. barthi* as is commonly believed in Europe. The upper limit for pes length in *C. barthi* is substantially below 15 inches.

A giant pes associated with a relatively small manus is described from the German Bunter as *C. barthi* var. *herculis* by Lilienstern (1939), and a similar pes is assigned to the *C. barthi* "group" by Soergel (1925). It is impossible to say at present whether the giant species of chirotheriid represented by the Bunter footprints is the same as *C. herculis* from the Keuper. The latter may be a giant species of large-manus chirotheriid for all one can tell from the original description of Egerton. Lydekker (1890) states that the pes of *C. herculis* resembles that of *C. storetonense* Morton, which appears from the original description to be a large manus chirotheriid.

Chirotherium storetonense Morton, 1863

Chirosaurus stortonensis (Morton) Lydekker, 1890.
[not] *Chirotherium storetonense* Soergel, 1925 (= C. beasleyi n. sp.)

The history of *Chirotherium storetonense* is complex. The species was first described from specimens in the Museum of the Royal Institution collected from Middle Keuper strata at the Storeton Hill quarry, Cheshire (Cunningham, 1839). Certain of the measurements are of critical importance; the pes is 9 inches long and digit IV is nearly as long as III and ¾ inch longer than II. The manus is 4½ inches long or *one half the length of the pes* and therefore relatively large. Cunningham refers to digit V as the "thumb," to IV as "toe 1," to I as "toe 4."

Morton (1863) refers to the original description by Cunningham and proposes the name *Cheirotherium storetonense*. This is accepted as valid by Lydekker (1890).

Beasley (1907) discusses the "Cheirotheroid forms" from the Storeton quarry.[3] He differentiates "a few rather large *Cheirotherium* prints" as group "*A* 1 = *Cheirotherium storetonense*." Certain other *Chirotherium* footprints previously included (Beasley, 1906) in his group *A* 4 are described further (fig. of manus and pes shown) and differentiated from group *A* 1 mainly by the possession of a very short pes digit IV, which is even shorter than pes II. The manus is merely referred to as "small" but the figure leaves no doubt of its tiny size relative to the pes; it is much smaller relatively than the manus measured by Cunningham. The latter's measurements (1839) prove Beasley entirely correct in differentiating group *A* 4 from *A* 1 (= *C. storetonense* Morton).

Lomas (1907) follows Beasley's paper with a description of a trackway composed of *Chirotherium* footprints "described by Mr. H. C. Beasley as *A* 4." The included figure showing 5 consecutive steps is the same one refigured by Soergel (1925) and Abel (1935) with the subtitle, "Fährtenfolge von *Chirotherium storetonense*, nach J. Lomas" (1907). Obviously an error has been committed. Soergel (1925) has given Morton's specific name to Beasley's group *A* 4 which has never had a specific name. Therefore, the new name *Chirotherium beasleyi* n. sp. is herewith proposed for the small-manus chirotheriid represented by group *A* 4 of Beasley (1906, 1907) and by the trackway described by Lomas (1907).

Ironically enough the specific characters of *C. storetonense* Morton are not nearly so evident from written descriptions as are those of *C. beasleyi* n. sp. As far as one can determine from Cunningham's measurements and from Beasley's description, *C. storetonense* Morton is apparently a large-manus chirotheriid with a long pes digit IV from the middle Keuper. However, a set of footprints figured by Lull (1904, pl. 72, *C* and *D*) from the Hitchcock Cabinet, specimen no. 26/25, and identified as "*Chirotherium storetonensis*" presumably from England's Storeton, has a strong resemblance to Beasley's group *A* 4.

[3] According to Dr. R. S. Lull (oral communication), casts of Beasley's specimens are in the Peabody Museum, New Haven, but I have not had the opportunity to study them.

Chirotherium parvum (Hitchcock)

Otozoum parvum Hitchcock, 1898.
Chirothorium? (Otozoum) parvum (Hitchcock) Lull, 1915.

The species is based on rather poor but definitely chirotheriid footprints from the Upper Triassic Newark Series of Eastern North America. The question mark may be removed from Lull's generic determination (1915), but the species is probably indeterminate.

Chirotherium gallicum (Bornemann MS.) Willruth, 1917

The original description published by Willruth (1917, p. 40) is from a manuscript of J. G. Bornemann and is based on a single set of footprints from the Bunter of Lodève. Differentiation from *C. barthi* is by virtue of a more slender fifth pes digit of which the phalangeal portion is straight instead of recurved, the metatarsal region is flatter and elongate posteriorly, a granular skin surface shows on all parts of the impression. Study of American specimens of *C. barthi* indicates that such characters are usually unreliable for specific determination. The clear photograph supplied by Willruth indicates that the single set of footprints known as *C. gallicum* is an unusually clear impression of *C. barthi*.

Chirotherium bornemanni Willruth, 1917

As described by Willruth (1917) this species from Harras near Eisleben is without question a synonym of *C. minus* Sickler. No attempt is made to differentiate the one from the other, and it is difficult to know exactly what is meant by "*Chirotherium Bornemanni* (*Ch. minus* Sickler) n. sp. ?" Photographs of specimens in the Geology Department of the University of Halle indicate that *C. bornemanni* resembles long-striding *C. minus* rather closely except for a marked difference in size. The latter has a pes length ranging from 8.5 to 12 cm. in different individuals, the former measures slightly under 5 cm.

Chirotherium pfeifferi Soergel, 1925

The description of the species consists of a photograph of manus and pes, obscure in detail, from Bockedra in Thuringia, an outline drawing of the pes and a statement that pes digit V bears a claw (p. 18, figs. 16, 17). The photographed pes resembles poor impressions of *C. minus* found in the Moenkopi. It is quite possible that *C. pfeifferi* Soergel is the same as *C. minus* Sickler.

Chirotherium hessei Soergel, 1925

The original description consists of a photograph of a clearly defined pes and an obscure manus from Kauerndorf near Kulmbach, a reconstructed pedal skeleton, and the statement that *C. hessei* is characterized by a relatively large manus and is a primitive type as shown by osteological reconstruction of the foot (figs. 12, 30; p. 32). Schmidt (1928) does not include this species in his catalogue of fossils from the German Triassic. Species which are included are: *C. barthi, sickleri, pfeifferi, bornemanni.* Nevertheless *C. hessei* seems to be a

distinct species. The pes is stout and broad with a relatively long digit IV and a peculiarly thick-set digit V. It is not represented among Moenkopi chirotheriids.

Chirotherium vorbachi Kirchner, 1927

This species is described from several footprints from the Upper Bunter of Gambach near Würzburg and of Aura near Kissingen. Specimens are in the Geological Institute of the University of Würzburg. The specific name is for Pastor Vorbach who first discovered the tracks in Franken. The best set of footprints (fig. 4) belongs to a trackway of three consecutive steps, one which was already determined as *C. barthi* by Soergel (1925, fig. 38). Differentiation of *C. vorbachi* from *C. barthi* rests mainly on the slenderness and recurved outline of the phalangeal portion of pes digit V. These characters and others used by Kirchner are likely to be influenced considerably by the size and gait of the individual and therefore the evidence for the new species is not conclusive.

Chirotherium bipedale Abel, 1935

First figured by Abel in 1912, this bipedal trackway from the English Keuper at Storeton was finally given the name *C. bipedale* (Abel, 1935). The well-known drawing would indicate that the original trackway represents a poorly recorded trackway deficient in precise characters of the feet. It resembles the trackway of a small manus chirotheriid found in the Moenkopi (cf. *C. marshalli*), which was poorly recorded and does not permit a specific designation. As such it would seem advisable to designate Abel's species as *Chirotherium* sp. indet.

Chirotherium thuringiacum Lilienstern, 1938

Description of the new species is based on large quadrupedal tracks from the Keuper of Germany originally assigned to *Plateosaurus* (Kuhn, 1938). Digit V is rudimentary and characteristically leaves a ball-shaped impression. The pes is as broad as long. *C. thuringiacum* cannot represent a typical chirotheriid, and the assignment of the species to the genus *Chirotherium* is open to question.

Chirotherium hildburghausense Lilienstern, 1939

The species is based on a poorly recorded trackway of nine consecutive steps from the German Bunter at Hildburghausen. The pes is 9 cm. long and appears to be of primitive pattern with a relatively long digit IV, and the manus is relatively large. The most distinctive character is the indefinite posterior border of pes digits I–IV.

Chirotherium angustum Huene, 1941

The species is described from a single pes impression 13.5 cm. long from the ? Keuper of northern Italy. The only distinctive character is a relatively small, short digit V.

Chirotherium beasleyi n. sp.

See page 345 for discussion of this designation for material collected in 1907.

Chirotherium kaupii

Mentioned by Morton (1863) as occurring at the Storeton quarry in the English Keuper. Further information is not available.

Chirotherium culmbachense

Mentioned by Soergel (1925, p. 73) and by Lilienstern (1939, p. 368). Further information is not available.

Chirotherium sp. indeterminate

Saurichnites auraensis Kirchner, 1927.

Isolated, poor pes impressions of *Chirotherium* which, lacking accompanying manus impressions, are considered to belong to bipedal reptiles and therefore are not *Chirotherium*. A trackway of such pes impressions is not demonstrated.

"Chirotherium" heterodactylus King, 1844

Supposed chirotheriid from the Carboniferous of Pennsylvania.

"Chirotherium" reiteri Moore, 1873

Supposed chirotheriid from the Carboniferous of Pennsylvania.

"Chirotherium" geinitzi Hornstein, 1876

The original description of this species from the German Bunter of Karlshafen is deficient, and the disposition of original specimens is uncertain. None of the generic characters of *Chirotherium* can be recognized in the description. The manus and pes appear to be of equal size. Lydekker (1890) lists the species as synonymous with *C. barthi;* Willruth (1917, p. 41) states that *C. geinitzi* is not a chirotheriid.

Large-Manus Chirotheriids from the Moenkopi Formation

Chirotherium diabloensis n. sp.

Type.—Univ. Calif. Mus. Pal. no. 36819, trackway of 24 consecutive steps (pls. 33, 34).

Paratype.—U.C.M.P. no. 36822, trackway of 9 and 7 consecutive steps (pls. 35, *A*, *B*).

Referred specimens.—U.C.M.P. no. 36820, 12 consecutive steps; no. 36823, 26 consecutive steps; no. 36826, 4 consecutive steps; no. 37777, 3 consecutive steps; no. 37321, isolated manus and pes with tail mark.

Horizon and locality.—Lower Moenkopi east of Canyon Diablo and near Meteor Crater, Arizona, U.C.M.P. loc. V3835, loc. map at "amphibian quarry," and at "c."

Diagnosis.—Trackway relatively wide for chirotheriids, pace angulation 140 degrees; maximum pes length 5.3 cm.; pes digit IV at least as long as III, pes digit V long and slender, without specialized pad.

Discussion

The new species represents the smallest chirotheriid yet known, and is based on the trackways of four different individuals. The trackways occur as casts on the underside of sandstone lenses; all trackways but no. 37776 came from the amphibian quarry; it came from the cap rock of a low butte across the road from the quarry, loc. map at "c," and from the same level.

The trackways afford an excellent opportunity to observe variations in the walking gait of several different individuals of the same species. These variations originate from two sources: physical character of the animal; extramorphologic characters such as differences in speed and in the condition of the recording surface.

No. 36819 (type), figs. 21, *C* and 22, *A*

The type trackway is the most clearly impressed of all except the paratype. The trackway crosses the surface with uniform stride. The 24 consecutive steps cover a distance of 310 cm. Each step consists of a set of manus and pes impressions with the small manus just in front of the pes in the chirotheriid manner. The trackway pattern is relatively wide for chirotheriids, the pace angulation being consistently 140 degrees. The stride increases from 26 to 29.5 then decreases to 24 cm. in 24 steps; 27 cm. is the average. The ratio of stride to pes length is low, about 5 to 1—as low as in lacertoid trackways but not for the same reason, as an analysis of body form will show.

The pes does not fall on the midline but is approximately .8 cm. from it. It is turned out 22 degrees (using III as the longitudinal axis). The manus is turned out a like degree instead of pointed forward as in most chirotheriids.

The pes is impressed fully with little distortion of its true character, but the manus usually shows only a strong impression of digits I–IV. The long series of footprints combine to give a clear portrait of the pedal morphology.

There is no tail mark associated with the trackway although near steps 17, 18, and 19 there is one which at first appears to be. It belongs instead, however, to the trackway of a running individual (no. 36820).

Character of manus and pes.—The feet are typical of *Chirotherium* in general outline. The pes is about twice the area of the manus and both have sharp claws on digits I–IV. These digits are grouped together; divergent digit V makes a separate impression. Digital pads are completely lacking. As a result some of the digits, particularly pes digits I–IV, show swellings at the joints and constrictions in the mesarthral areas as in recent lizards. All the digits are relatively slender compared with the thick-toed giant forms.

Manus: The manus is 2.8 cm. long by 2.0 cm. wide overall. Digits I–IV diverge within a 60-degree angle. Digit I is very small, II and IV subequal, III the longest. All are relatively short compared with the same digits of *C. cameronensis*. Small sharp claws about .2 cm. long are present but they do not show up clearly in most impressions.

Manus digit V is thumblike but straighter than pes V. Its impression is free from digit group I–IV, unlike the bunch-fingered manus of *C. coltoni* and *marshalli*. The phalangeal formula is not indicated although in an isolated manus from another trackway (pl. 35, *C*) gentle swellings at the joints indicate a 2–3–4–?–? formula. Faint detail of a granular skin surface can be seen in the better impressions.

The animal walked with pressure mainly exerted on digits II–IV so that a complete impression such as shown in figure 22 is unusual.

Pes: The pes is 5.3 long $\times$ 3.0 cm. wide overall.

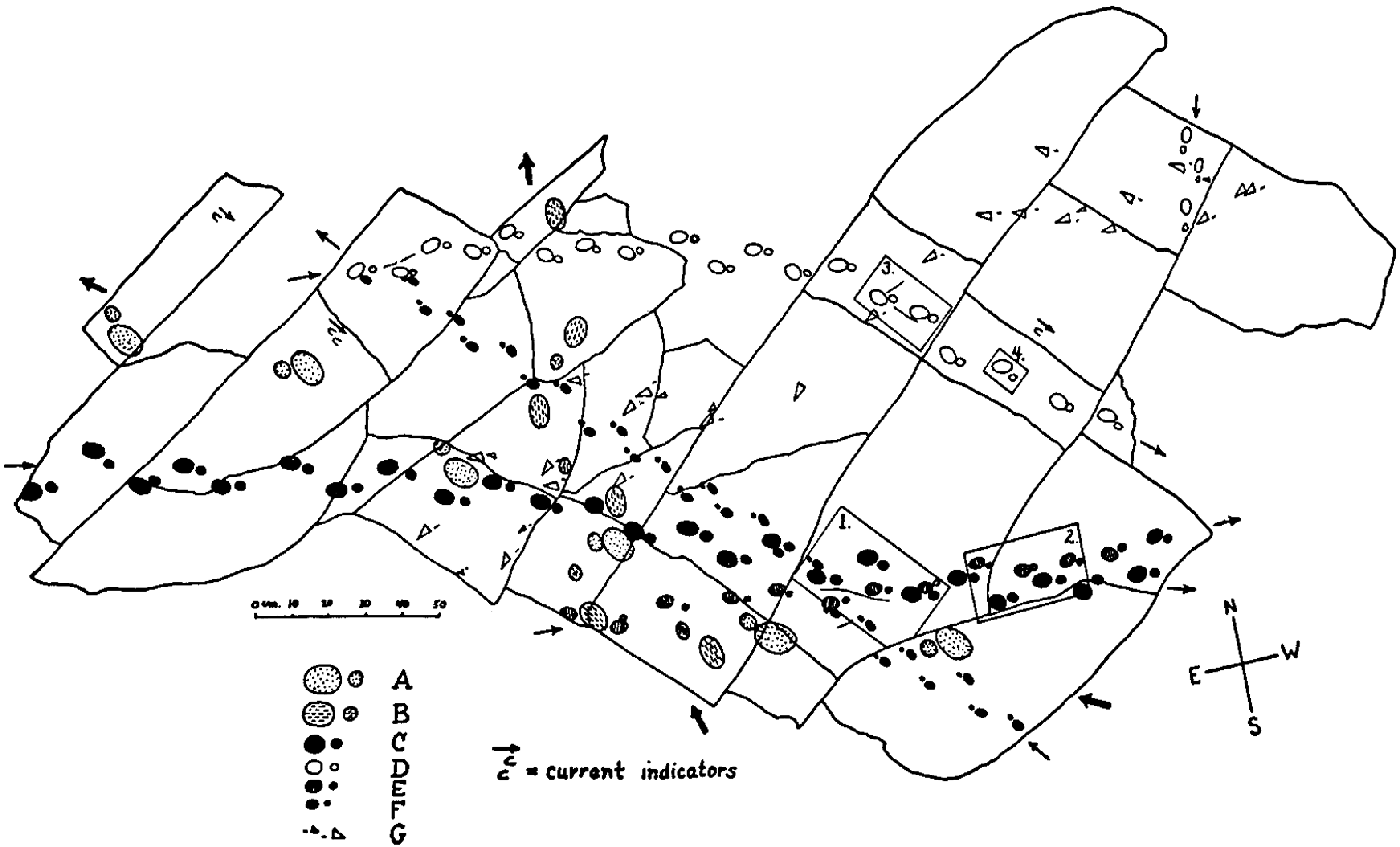

Fig. 21. Diagram of trackway surface (cast) from the amphibian quarry in the Lower Moenkopi near Meteor Crater: *A* and *B*, *Chirotherium minus*; *C–F*, *Chirotherium diabloensis*; *G*, *Rotodactylus cursorius*. Rectangles 1, 2, 3, and 4 are shown in pls. 33, 34, and 35, *A* and *B*, respectively.

Digit IV is at least as long as III and appears to be even longer because of the marked slant of the metatarsal-phalangeal axis. Distortion caused by walking tends to elongate the impression still more. The other trackways prove beyond a doubt that digit IV is relatively long in *C. diabloensis*, longer than in other chirotheriids except *C. cameronensis*. This must be considered a primitive character since there is a general tendency toward a reduction in the length of pes digit IV among chirotheriids. Digit I is about half the length of II, the latter slightly over half the length of III. Thus the progressive increase in length from digit I to III is marked.

The cross axis makes an acute angle of 55 degrees with the long axis of the foot (parallel to III); in other chirotheriids except *C. cameronensis* the angle

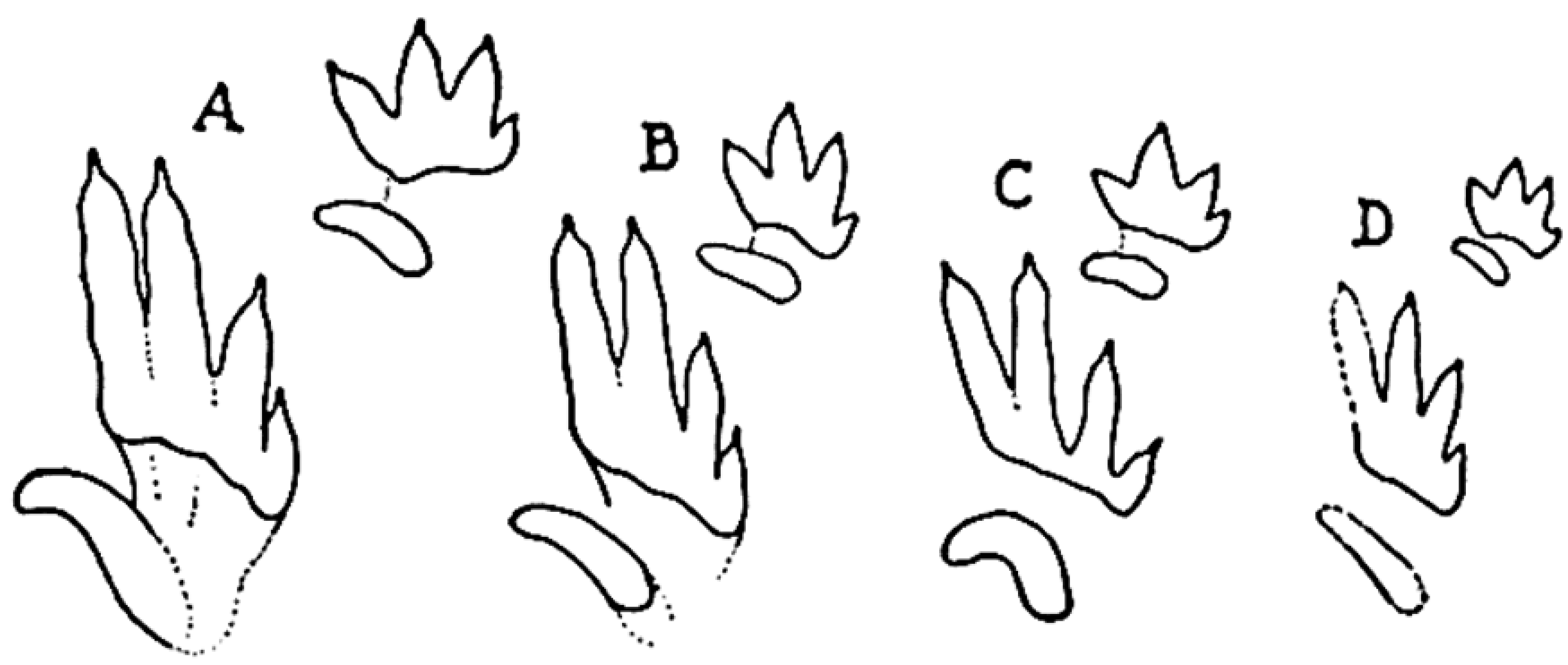

Fig. 22. *Chirotherium diabloensis;* manus and pes impressions from four different trackways shown in fig. 21: *A*, no. 36819 (type), fig. 21, *C; B*, no. 36822 (paratype), fig. 21, *D; C*, no. 36820 (running trackway), fig. 21, *E; D*, no. 36823 (? juvenile), fig. 21, *F*. × ½.

approaches 90 degrees. This character is also considered primitive for it resembles the condition in the lacertoid foot of the Protorosauria and other reptiles where the metatarsals are progressively longer from I to IV.

Pes digit V is long and slender and not enlarged proximally by a metatarsal pad as in all other species except *C. cameronensis*. However, the last named species has a *short* slender pes digit V. The absence of a metatarsal pad on digit V is probably primitive, but the relation of size of animal to development of this pad is not fully understood. Increase of body size in one species seems to be partly correlated with enlargement of the pad (*C. barthi*), but there is no evidence that the young (small individuals) of any species lack a pad that is present in the adult (large individuals). For example, newporn pigeons have all the digital pads developed precisely as in the adult although they may be less calloused.

Digits I–IV diverge within a relatively small angle, 15 degrees; III and IV tend to parallel each other. Narrow, sharp claws about .4 cm. long and .2 cm. wide at the base are present on digits I–IV. The claw impressions are subject to secondary elongation by foot movement and also by cracks developed in the recording surface.

The phalangeal formula, 2–3–4–5, is indicated in digits I–IV by swellings at the position of the phalangeal joints as in the pes of a recent lizard. The identity of the fourth phalanx (penultimate) in digit IV is not clear but the length of the first, second, and fifth (terminal phalanx) can be measured and indicates conclusively that there is adequate room for a third and fourth pha-

lanx between the second and fifth.[4] Pes digit V gives no direct indication of the number of phalanges in spite of the lack of a metatarsal pad. The flexibility noted in recurved impressions suggests that there are at least 3 phalanges in the distal two thirds of the impression.

The pes is impressed more strongly on the median side but not to the extent seen in the paratype.

TABLE 6

STRIDE AND PACE ANGULATION IN *C. diabloensis*[a]

Step	No. 36819, type (walking)		No. 36822, paratype (slow to fast walk)		No. 36820 (running)		No. 36823 (walking)	
	Stride	P. A.	Stride	P. A.	Stride	P. A.	Stride	P. A.
1–3	25.5	....	19.5	144°	28.7	....	14.6	116°
2–4	26.5	....	19.5	135°	(29.5)	....	14.6	116°
3–5	28	....	20.8	143°	(29.5)	....	16.5	128°
4–6	27.5	....	22.5	....	(29.5)	....	....	....
5–7	27.5	....	22.2	....	27.5	....	....	....
6–8	27.5	....	21	....	28	150°	....	....
7–9	27.5	....	24.5	....	27	162°	16.7	116°
8–10	27.5	....	....	....	25.5	....	....	....
9–11	29.5	137°	....	....	25.5	....	....	....
10–12	28	....	....	....	25.5	184°	....	....
11–13	27	....	....	....	....	....	....	....
12–14	....	....	....	....	....	....	....	....
13–15	....	....	....	....	....	....	....	....
14–16	....	....	24.2	150°	....	....	....	....
15–17	....	....	25.2	....	....	....	....	....
16–18	....	....	29.7	....	....	....	....	....
17–19	27	142°	32.1	163°	....	....	....	....
18–20	26	138°	....	....	....	....	....	....
19–21	25	....	....	....	....	....	....	....
20–22	24.5	....	....	....	....	....	15.2	113°
21–23	24	....	....	....	....	....	15.2	111°
22–24	25.5	....	....	....	....	....	....	....
23–25	....	....	....	....	....	....	....	....
24–26	....	....	....	....	....	....	....	....

[a] Measurements given above are selected from complete records. Distances are in centimeters.

No. 36822 (paratype, figs. 21, *D* and 22, *B*)

The paratype consists of the first 9 and last 6 steps of a long clearly impressed trackway running more or less parallel to the type. Steps 10–13 are missing because the blocks containing them were not collected. The impressions of the feet are somewhat smaller than those of the type but otherwise identical.

The proportions of the trackway differ a little from the type. The stride steadily increases from 19.5 to 32 cm., and the pace angulation increases from about 140 to 158 degrees, indicative of a substantial increase in speed. (The

[4] For example, .9 (1) + .6 (2) + .7 (5) = 2.2 cm. which leaves .8 cm. since the five phalanges total 3.0 cm. Therefore phalanx 3 and 4 were probably each 4 cm. long.

average stride of the type trackway is 27 cm.) The manus impression is variable in its position relative to the pes. As the stride increases the manus moves backward and inside (medial) of the pes in consecutive steps.

The pes is deeply impressed on the inside, particularly in the first steps where the stride is short. Digit IV is faintly impressed. The pes is turned out more than in the type, 30 compared with 22 degrees. The characters noted are probably variations in the gait of similar individuals.

TABLE 7

MEASUREMENTS OF MANUS AND PES IN *C. diabloensis*
(in centimeters)

Measurements	No. 36819, type	No. 36822, paratype	No. 36820	No. 36823
Manus: L.	2.8	2.4	....	1.6
W.	2.0	1.7	(1.7)[a]	1.2
Pes: L.	5.3	4.8	3.8	3.5
W.	3.0	2.5	2.5	1.8
Length of manus:				
I.	.7	.8	...	.6
II.	1.4	1.2	.9	.85
III.	1.7	1.4	1.2	.9
IV.	1.4	1.1	...	.6
V.	1.4	1.3	...	(.7)
Length of pes:				
I.	1.4	1.6	1.1	.8
II.	2.2	2.3	1.6	1.6
III.	3.1	2.8	2.4	2.2
IV.	3.1	2.6	2.3	2.2
V.	2.0	1.7	1.2	(1.6)
Length of phalanges of pes (proximal to distal):				
I.	.4–.4			
II.	.8–.6–.7			
III.	.9–.7–.5–.7			
IV.	.9–.6–.4–.4–.7			
V.	?.5–?.3–?.4			

[a] Figures in parentheses are estimated.

The presence of tail marks associated with trackways of chirotheriids is infrequent in the Moenkopi and unknown elsewhere. Tail marks have been noted in Europe (Boule and Piveteau, 1935, p. 5) but not found directly associated with a trackway pattern. The paratype exhibits two short marks. Just in front of the manus of step 2 a thin ridge extends forward 9.5 cm. more or less continuously toward the heel of the pes in step 4. The tail mark runs to one side and slightly oblique (7 degrees) to the midline. The ridge is very narrow, about .1 cm. wide, and undoubtedly represents the keeled ventral surface of the tail of the animal which made the trackway. Another tail mark, 4 cm. long,

runs parallel to the midline and medial to the pes of step 16. By coincidence a tail mark of another reptile, *Rotodactylus*, crosses the chirotheriid trackway at right angles near step 15 (pl. 35, *A*).

No. 36820, figs. 21, *E* and 22, *C*

A trackway of 13 consecutive steps crosses the type trackway obliquely near step 19. The trackway is poorly impressed compared with the ones just described. The feet of the animal penetrated the thin marl so that many of the footprints are undecipherable blobs.

The stride and pace angulation are relatively large, 27 cm. and 16 degrees, respectively, considering that the feet are definitely smaller than in the type or paratype.

The manus impression occurs with variation on the midline just ahead and inside the pes. In steps 2 and 6 it is directly median to the pes. The impressions tend to be tridactyl (digits II–IV) but digit I and V may be distinguished in the deeper ones. Divergence of digits I–IV from each other is no different from type and paratype.

The pes impression differs from the type and paratype by exhibiting a marked divergence of digits I–IV, 35 degrees compared with about 15 degrees, and a strongly recurved digit V. The long axis of the pes is nearly parallel with the midline, instead of oblique and closer to the midline with digit I falling directly on it. The differences noted above indicate differences in the walking and running gait of chirotheriids of the same kind if not of the same size. The factor of increased speed has operated here to cause considerable variation in the trackways of one species. Several facts stand out in a running trackway: the pes turns in more and is closer to the midline, pes digits I–IV spread widely, pes digit V is forced into an abruptly recurved position, and the manus continues to function in a purely quadrupedal gait.

The tail mark associated with steps 6 and 7 coincides with the general direction of the trackway. At first glance the mark might be wrongly associated with the more clearly impressed type trackway. The tail mark is 17.5 cm. long; it begins medioposterior of the pes in step 6, extends for 8 cm. in the direction of progress, then curves broadly to the left and begins to straighten out as it terminates medial to the pes of step 7. Discontinuity in the tail mark was caused by an uneven recording surface. The mark is narrow and as in the paratype trackway indicates the presence of a sharp ventral keel on the tail. The character of this and previously described marks indicate that the tail was long but was habitually carried free of the ground in a balancing position (cf. Structure of *Chirotherium*).

No. 36823, figs. 21, *F* and 22, *D*

A poorly recorded trackway of 26 consecutive steps crosses the surface about parallel to the type but in the opposite direction. One may puzzle out the successive steps with the blocks of the trackway surface all assembled but short sections of the trackway are unintelligible unless the continuity is established. The footprints are very small, about one half the size of the type but otherwise

similar in character. The manus regularly occurs just ahead of the pes. Most of the footprints are mere blobs on the surface, but certain steps, particularly 9 and 17, clearly establish the essential details.

The stride and pace angulation are 15 cm. and 117 degrees, respectively. The manus and pes average 1.5 cm. from the midline so the pattern is relatively wider than the other trackways of *C. diabloensis.*

The pes is turned out an average of 30 degrees from the midline, and the habit of walking with the pressure mainly on the inside of the pes, as noted in the paratype, is consistently shown in all steps. As a result pes digits I–III are the only ones to impress consistently. The thin marl was not favorable for a clear record of this small animal. Apparently the type trackway represents the optimum size for clear impression on such a surface.

Relationships

The four trackways described above were probably recorded by individuals of a local population of one species of chirotheriid. The interpretation that the trackways represent four individuals gains support from the occurrence of similar size range in trackways of *C. minus* and *C. barthi.* In all three species several trackways occur *on the same surface* and are similar except for size. In each species the range in size is roughly a factor of 2, the largest trackway being about twice the size of the smallest. Other characters being equal, it is safe to assume that the local population of any one species consisted of individuals of different stages of growth. The alternative assumption that each trackway represents a different species is unnecessary and unwarranted. Most of the differences can be attributed to variation in body size, speed of locomotion, and in the character of the recording surface.

C. diabloensis represents a new and relatively primitive chirotheriid of small size. The trackway pattern is relatively wider than in other chirotheriids and the pes is primitive in its possession of a long digit IV and of an oblique metatarsal-phalangeal axis of lacertoid character. The lacertoid habit of impressing the median border of the pes more strongly than the lateral border is particularly noted in two trackways.

A primitive foot plan is also found in the Upper Moenkopi species, *C. cameronensis*, but the latter represents a rangy, long-striding reptile with a narrow trackway, to mention only a few differences. The two species cannot be confused with each other and neither one can be confused with known chirotheriids from Europe.

A possibility that *C. diabloensis* is the young stage of contemporaneous *C. minus* has been considered but not held likely because of important structural differences in the feet.

Chirotherium cameronensis n. sp.

Type.—Univ. Calif. Mus. Pal. No. 37316, trackway of 4 consecutive steps (pl. 36).

Referred specimen.—Isolated manus and pes impression on slab containing type.

Horizon and locality.—Upper Moenkopi southwest of Cameron, Arizona, U.C.M.P. loc. V4204 (see locality map). The large slab of sandstone which contains the trackway of *C. cameronensis* also contains a set of excellent footprints of *C. barthi* (pl. 40, *A*).

Diagnosis.—**Relatively narrow, long striding trackway, pace angulation 180 degrees; pes length 5 cm., pes digit IV as long as III, digit V short and slender without specialized pad; manus digits I–IV relatively long, pes digits relatively widespread.**

Discussion

The small animal which made the trackway walked on a straight line. The two strides are 43 and 42 cm. (3 paces are 21.7, 20.3, 20.0 cm.) and the pace angulation is 161 and 162 degrees. Both stride and pace angulation are relatively large. The overall size of manus and pes is 3.0 cm. long by 2.7 cm. wide and 5 cm. long by 3 cm. wide, respectively.

The manus occurs just in front and inside of the pes but is not overlapped. It is turned inward so that its longitudinal axis (III) parallels the midline. By contrast the pes is turned out 13 degrees (av.). The manus occurs close to the midline, less than .5 cm. (av.) and the pes is even closer, .3 cm. (av.). The impressions are not pronounced but the succession and principal characteristics are clear. There is no evidence of a tail mark. The trackways must be studied with lighting directed from various low angles. A photograph fails to show detail unless a weak impression is oriented at right angles to the light source; for example, manus digit V, step 1, seems to be absent in the photograph but is not.

Manus.—The manus is relatively large and long for *Chirotherium*, 3. long by 2.3 cm. wide, overall, by reason of long slender digits I–IV, 1.2, 1.6, 2.0, 1.7 cm. long, respectively. Digit I is only faintly indicated in contrast with the strong impressions of II–IV. These digits have short narrow claws. The total divergence of I–IV ranges from 37 degrees in step 1 to 70 degrees in steps 2, 3, and 4. Digit III and IV are separated slightly more than the others. The metacarpal-phalangeal axis is not so deeply impressed relative to the carpal region as in other chirotheriids. This is also true of the pes.

Digit V is relatively short compared with digit III and more slender distally than in *C. diabloensis*. The tip is clearly impressed in step 4 and seems to be clawed. One cannot be sure that this is so from evidence of the other 3 manus impressions.

Pes.—The general plan of the pes is somewhat like *C. diabloensis* from the Lower Moenkopi. The digits are long and slender and have no marked development of digital pads. Digit IV is as long as III and the metatarsal-phalangeal axis is strongly oblique, 55 degrees, to the long axis of the foot. Here the similarity ends. Digits I–V measure 1.3, 2.5, 3.0, 3.0, 1.5 cm., respectively. Digits I–IV diverge from each other 43 degrees in step 1 to 30 degrees in step 4, an amount comparable with the running trackway of *C. diabloensis*. But there is no evidence to show that the trackway described here is a running trackway. The high degree of divergence would seem to be a real character, then, instead of one caused by a running pace. The one isolated pes impression on the same surface also shows a digital divergence of 30 degrees. Digits II–III are noticeably curved, convexly outward, in contrast with the straight digits of all trackways of *C. diabloensis*.

Digit V is relatively small, recurved, and set well back from digit group I–IV.

Its proximal part is not expanded by a pad and thus with *C. diabloensis* differs from other species. Its position is unique in that it is placed more nearly under the metatarsal region. In all other chirotheriids the base of digit V is never entirely medial to a line extended backward from the lateral border of digit IV as it is here.

The character of the metatarsal region shown in step 1 is particularly revealing. It converges, wedgelike, toward the base of digit V, giving a triangular outline suggestive of a lacertoid pes. The proximal part of V passes smoothly into the posterior metatarsal region as in *C. diabloensis*, but the area of the heel is narrower. The line of metatarsal-phalangeal joints (I–IV) is not so deeply impressed relative to the metatarsal area as in *C. diabloensis* or *C. minus*. Also the posterior border of digit group I–IV in both manus and pes, though broadly indented, is complicated by bulging outlines of the base of the individual digit. This detail is well developed also in the giant species, *C. rex* and *C. moquiensis*.

The phalangeal formula is not indicated in either manus or pes. Although slender, the digits fail to show the knoblike enlargements occurring in the primitive species from the Lower Moenkopi. In the manus impression of step 1, transverse narrow furrows in digits II and IV suggest the division lines between digital pads. The distal half of pes digits III and IV is slightly bulbose, probably as a result of movement of the foot in the impression.

Relationships

The trackway of *C. cameronensis* shows a mixture of advanced and primitive characters. The trackway pattern, that of a walking animal, is quite narrow and the stride is long, 8.5 times the length of the pes and comparable to *C. minus*. The ratio of stride to pes length is only 7 to 1 in the running trackway of *C. diabloensis*, 5 to 1 in the walking trackway. The shape of the foot impressions, particularly the fullness of the manus impression, clearly indicates a walking pace, so the narrow pattern and long stride did not result from a running pace. The proportions of the trackway pattern indicate a long-limbed, slender animal which walked with the limbs well under the body, and closer to the midline than in *C. diabloensis*.

The manus is turned straight forward and not outward as in *C. diabloensis*, but the pes is turned out to a comparable degree. The large, long-fingered manus probably represents the primitive condition among chirotheriids because the general tendency is toward a small short manus with all 5 digits bunched together.

The pes is primitive in the possession of a long digit IV, an oblique cross-axis, and a slender digit V which lacks the expanded base of the specialized forms. Yet digit V is relatively small and short, and is unique in its position, almost directly under the metatarsal bundle. It apparently supported or propped the foot more directly than in most other chirotheriids. This is the only pedal character which can be termed "advanced." Except for the fifth digit the pes has a lacertoid appearance.

C. cameronensis cannot represent the very young stage of contemporaneous

forms (*C. barthi* occurs on the same surface) because of the very different proportions in the manus and pes. The occurrence of a species with a curious mixture of advanced and primitive characters in the Upper Moenkopi is no less strange than the occurrence of an obviously specialized, small-manus species, *C. coltoni*, in the Lower Moenkopi of Meteor Crater. The seeming paradox can possibly be explained by the presence of a large number of species of chirotheriids, a small sample of which left records on the mudflats. On the basis of pedal structure alone, *C. cameronensis* would seem to be at least as primitive as *C. diabloensis*.

Chirotherium minus Sickler, 1836

Chirotherium minus gen. indet. Lydekker, 1890.

Chirotherium bornemanni Willruth, 1917.

Chirotherium sickleri Soergel, 1925.

Type.—Not designated by Sickler; considered here to be represented by Winkler, 1886, p. 430, pl. III (2), and pls. IV and VI which show Musée Teyler (Belgium) slab specimens nos. 1320 and 1317.

Referred specimens.—Univ. Calif. Mus. Pal. no. 37309, trackway of 9 consecutive steps; no. 36824, 6 consecutive steps; no. 36825, 6 consecutive steps; nos. 36828, 37327, 37331–34, 37339, 37772–76, isolated impressions of manus and pes contributing important detail.

Horizon and locality.—Lower Moenkopi near Meteor Crater, Arizona, U.C.M.P. loc. V3835, locality map at "amphibian quarry" and at "a" and "c."

Diagnosis.—Relatively narrow, long-striding trackway, pace angulation 160 degrees; pes length maximum 12.2 cm., av. 9 cm., pes digit IV subequal to III but considerably longer than II, digits without specialized pads except pes digit V, which has small pad at position of metatarsal-phalangeal joint; manus digit IV shorter than III, digit V variable in its position. Consecutive pes impression somtimes show occasional absence of digit V.

Discussion

This medium-sized chirotheriid is associated with *C. barthi* in the Bunter of Hessberg. Although the original description is deficient, excellent figures of its trackways are published by Winkler. Lack of pes digit V in British Museum specimens caused Lydekker (1890) to relegate *C. minus* to "genus indet." The species *C. bornemanni* Willruth (1917) seems to represent an unwarranted attempt to rename the original species of Sickler. *C. sickleri* Soergel (1925) is considered here a synonym because a comparison of Winkler's description and plates with Soergel's figures 21 and 23 shows perfect agreement of definitive characters. Also the slab in Soergel's figure 23, which shows "*C. sickleri*" associated with *C. barthi*, is from Hessberg, as are the Musée Teyler specimens figured by Winkler, which are also associated with *C. barthi*.

No. 37309, figs. 16, 17, 23, pl. 37

This trackway of 9 consecutive steps is preserved on the underside of a series of 10 sandstone slabs. Two consecutive steps representing a continuation of the trackway are shown in fig. 17. The slabs are from the butte south of the amphibian quarry (loc. map at "a"), and they preserve in perfect detail a Triassic record originally made in red mud. The reptile which made the trackway walked with uniform pace straight across a surface cracked by desiccation.

None of the footprints seem to be widened secondarily by the cracks which run through them. There is no tail mark associated with the trackway.

The stride and pace angulation are 75 cm. and 164 degrees (av.), respectively. The pes occurs close to the midline, .5 cm. (av.), and is turned forward so that digit IV makes an angle of 12 degrees (av.) with the midline. The manus occurs just in front and inside of the pes with its median margin approximately on the midline. It is turned inward so that digit III points directly forward.

The footprints are variable in their completeness, particularly the manus. Pes digits I–IV are clearly impressed in each step but V fails to show in steps 2, 3, and 6. Manus digits I–IV are clearly impressed in all steps but no. 3. Digit V appears only in the more deeply impressed steps 5, 7, 8, 9. Both feet show claws on digits I–IV. Variations in the degree of impression may have been caused by variations in the original recording surface, although the sporadic absence of pes digit V seems to have been caused by a peculiarity of gait (cf. Structure of *Chirotherium*).

Fig. 23. *Chirotherium minus*; manus and pes based on composite detail of trackway no. 37309 (pl. 37, figs. 16, 17). × ½.

The trackway is relatively narrow and the stride large; the ratio of stride to pes length is 9 to 1. The consistently stronger impression of the front part of both manus and pes might indicate a hurried walk or almost a running gait. However, the occasional lack of pes digit V in the impression is also characteristic of the species in Europe, so the trackway probably is of a walking, not a running animal.

Manus.—The manus measures overall 4.4 cm. long by 3.2 cm. wide; digit group I–IV measures only 3.0 cm. long by 2.4 cm. wide. Digits I–IV are bunched closely together in all impressions, unlike the specimens described later, and the division lines between them are blurred. Digit I is about half the length of III; IV is two thirds the length of III and noticeably shorter than II, unusual for chirotheriids. Digits I–IV are relatively longer than other species except for *C. cameronensis* from the Upper Moenkopi, and IV is relatively shorter than any.

Digit V diverges strongly outward 80 degrees from III. Where deeply impressed it is lenticular in outline (step 5) and its base merges smoothly into the surface of the palm.

There is no deep groove running between it and the base of the other digits. In steps 5 and 7, digit V seems to have had a claw but this is apparently due to cracks in the recording surface originating from the digit tip. Short narrow claws with blunted ends were present on digits I–IV.

Pes.—The pes measures overall 8.5 cm. long by 5.2 wide; digit group I–IV measures 7.0 cm. long by 4 cm. wide. Digit IV is subequal to III, which is the longest; I is less than half the length of III and about two thirds the length of II. All four had long narrow claws with blunted ends. The metatarsal-phalan-

geal axis is less oblique to the longitudinal foot axis (70 degrees) than in *C. diabloensis* (55 degrees), but more oblique than in larger chirotheriids.

The impression of digit V is separate from the other digits and the expanded base lies outside the center line of IV. Digit V is characterized by a threefold division: a moderately expanded base representing a metatarsal-phalangeal pad, a narrow central region, and a sharply bent, rather than recurved tip. The expanded base is intermediate in size between the primitive unexpanded

TABLE 8

Comparative Measurements of the Three Trackways of *C. minus*

Measurements	No. 37309	No. 36824	No. 36825
Stride, in centimeters:			
1–3	76	99	46
2–4	79	96	50
3–5	73	94	45
4–6	72	95	51
5–7	76	..	..
6–8	..	..	..
7–9	..	..	..
Pace angulation, in degrees:			
1–2–3	...	152	98
2–3–4	163	174	130
3–4–5	161	124	114
4–5–6	167	157	149
5–6–7	165	...	...
Pes, in centimeters:			
Width	5.2	8.0	5.2
Length	8.5	12.2	9.4
Stride—pes length ratio	9 to 1	8 to 1	5 to 1

condition in *C. diabloensis* and the more massive expansion of large species such as *C. barthi*.

With the exception of the expanded base of digit V, the digits of the pes are lacking in the obvious development of specialized pads. Perhaps the most characteristic feature in the pes is the knobby contour of digit IV. The lateral pressure exerted on the pes brought the skeletal framework into sharp relief. In this manner the identity of the first four phalanges of digit IV are characteristically indicated by alternating bulges and constrictions.

Measurements of trackway no. 37309 and of the supplementary material are contained in tables 8 and 9.

Most of the American material representing *C. minus* came from the amphibian quarry at Meteor Crater. Trackways and isolated footprints were originally recorded in thin slippery marl which apparently stuck to the feet of the reptiles and resulted in blobbed impressions.

No. 36824, 6 consecutive steps, fig. 21, *A*

The largest trackway associated on the same surface with *C. diabloensis* is not clear in detail of the feet; the animal walked nearly straight across the thin slippery marl of the original surface. The pace angulation is high (164 degrees av.) and the stride is relatively long compared to the length of the pes, as may be seen in trackway no. 37309.

TABLE 9

LENGTH OF DIGITS I–IV AND FIRST PHALANX OF IV IN *C. minus*
(in centimeters)

Specimen	Digits					Phalanx 1 digit IV
	I	II	III	IV	V	
No. 37309 (trackway)	2.7	4.7	6.1	5.5	3.3	1.5
No. 37325	...	5.5	7.5	6.5	3.7	1.8
No. 37327	2.9	4.9	6.2	...	...	1.6
No. 37331	3.3	5.2	6.5	5.5	...	1.7
No. 37334	...	4.6	7.8	6.9	4.2	1.8
No. 37339	...	...	...	...	4.1	1.7
No. 37772	...	...	...	...	3.9	1.6
No. 37773	...	4.8	6.7	6.0	3.5	...
No. 37774	...	(6.3)	...	...	3.5	1.8
No. 36824 (trackway)	(4.2)[a]	(6.1)	7.7	6.9	5.1	...
No. 36825 (trackway)	3.1	5.1	6.7	5.4	3.7	...
No. 36828	3.5	5.2	6.9	6.4	...	1.7
No. 37332	...	...	7.2	6.2	(4.1)	1.8
No. 37333	2.9	5.2	6.3	5.7	3.8	1.5
C. sickleri Soergel, fig. 21	3.1	4.5	5.9	5.1	3.2	...

[a] Figures in parentheses are estimated.

The grouping of manus and pes is normal for *Chirotherium* and both feet are oriented with the midline as in no. 37309. Although all the impressions are badly blurred, the general outline of the pes in particular indicates a close similarity with no. 37309 except for size. The pes is approximately one third larger. In spite of the poor impressions the knobby character of digit IV is clearly shown.

A number of isolated but very clear impressions of manus and pes on the same surface show practically the same characters as no. 37309, thus strengthening the diagnosis of the trackway described above.

No. 36825, 6 consecutive steps, fig. 21, *B*

A very irregular trackway about the size of no. 37309 crosses all the other trackways on the amphibian quarry surface. The impressions are generally poor but somewhat better than in the large trackway no. 36824. The pace angulation is irregular (98, 130, 114, and 149 degrees), as is also the stride (46, 50, 45, and 51 cm.). To these irregularities is added a marked variation in

the position of the manus relative to the pes. Taken together these surely mean that the trackway represents a slow hesitant walk associated with foraging or explorative actions on the part of the animal.

In the manus, digit group I–IV can be made out satisfactorily in general outline, but digit V seems to be quite variable in actual position as well as in manner of impression. A mobility or flexibility of V beyond that seen in other species is indicated in this trackway and proved in the isolated impressions discussed below. The pes is clear enough in steps 1, 5, 6 to show its general similarity to no. 37309 and to the clearer, isolated impressions from the same surface.

Isolated Manus Impressions

The isolated impressions of the manus add not only detail to the foot structure of *C. minus*, but also clearly show the presence of a remarkably mobile manus digit V. It was possible for the digit to rotate from an acute to an obtuse angle relative to III. The manus impressions in plate 38, *A* and *B* illustrate both extremes; other specimens show intermediate positions. The contour of the impression also varies noticeably in the different positions. These differences are interpreted as a characteristic of the species because all other characteristics are constant.

The 30-degree divarication of digits I–IV is 10 degrees more than shown in no. 37309 but is still small in comparison with other chirotheriids. The difference of 10 degrees could be attributed to individual variation and to differences in the recording surface. The short length of digit IV is definitely established in the clearer impressions.

The contours of the digit impressions, unlike those of the pes, give no clue to the phalangeal formula except in one specimen (no. 37340, pl. 38, *B*). The length of phalanx 1 of digit IV is indicated by slight prominences. Digital pads are not positively indicated in any impression.

Isolated Pes Impressions

The isolated impressions of the pes contribute a very clear picture of the skeletal framework of digits I–IV, less clearly of V. (cf. Structure of *Chirotherium*, p. 396). The phalangeal formula is 2–3–4–5–3(4). As a rule the enlargements at the joints in digits I–III and at the terminal joint of IV are blurred by shifting of the foot in the impression. Characteristically, as in no. 37309, the lateral border of digit IV shows four bulges corresponding to the first four joints. Phalanx 4 and the terminal claw phalanx are reduced so they are rarely indicated as separate entities in the impression. This is logical because the impression of digit IV is more often distorted than are the others.

In all the pes impressions there is a tendency for digit IV to be distinctly separated from III so that the division line is apparent nearly down to the metatarsal-phalangeal joint. Often a circular pit appears here (pl. 38, *C* and *E*), apparently because the knobs of the first phalangeal joint of digits III and IV touch each other.

The foot which made the impressions surely lacked any kind of digital pad on digits I–IV and the skin itself must have been thin and flexible to permit

the region of the joints to impress so clearly. Digit V shows the same threefold nature as seen in no. 37309 and in addition indicates a small degree of mobility. The median margin of the expanded base may lie inside the axis of IV, or outside as in no. 37309, and the separation of digit V from the base of IV may vary from 0 to .6 cm.

In all impressions the tip of digit V appears to bend sharply as if at a joint. On specimen no. 37772 (pl. 38, *C*), which has a very deep and concise impression of digit V, the contour around the anterior border of the distal one third is broken by two angles which are interpreted as the position of two phalangeal joints. Thus phalanx 1 would extend from the center of the expanded base to the first angle, phalanx 2 between the 2 angles, and phalanx 3 would complete the digit. Since no one has ever found a well-developed claw on pes digit V of *Chirotherium*, it may be that a small aborted terminal fourth phalanx was present. This cannot be proved from the excellent American material. Even if allowance is made for distortion of the impression, the third phalanx does seem rather long relative to the second phalanx as shown by other specimens, for example, by no. 37332 (pl. 38, *E*). Further discussion and reconstruction is presented under "Structure of *Chirotherium*."

Relationships

The trackways and isolated footprints described here represent the American equivalent of *Chirotherium minus* Sickler of Europe, so far as can be judged from written descriptions, from excellent drawings of Musée Teyler specimens (Belgium) published by Winkler (1886), and from good photographs of isolated footprints called *C. sickleri* by Soergel (1925). As mentioned earlier, *C. minus* was apparently described originally from footprints which lacked the impression of pes digit V. Footprints having the impression of pes digit V were described later as *C. sickleri* by Soergel (1925).

The trackway of *C. minus* represents a long-striding, slender-bodied chirotheriid which differs in a number of structural features from all other species known from the Moenkopi.

The stride is relatively longer than any species but *C. cameronensis;* the body size is intermediate between the small species described above and *C. barthi;* the feet are long-toed and, but for one exception, lack specialized digital pads.

The manus is characterized by a relatively short digit IV and by a digit V of variable position. The pes is characterized by knobby contours of digit IV which is definitely shorter than III but substantially longer than II. Pes digit V shows a small pad at the metatarsal-phalangeal joint and a definite threefold division into proximal (the pad), central, and distal thirds.

C. minus is of particular interest because of its habit of walking with the emphasis on digits I–IV of the manus and especially the pes. The fully developed pes digit V did not always touch the ground in the walking gait in contrast with the general tendency of all other chirotheriids to settle back on the heel of the pes.

C. minus is intermediate between the small primitive *C. diabloensis* and *cameronensis*, and large chirotheriids such as *C. barthi* and *marshalli* in certain

characters: length of pes digit IV, obliqueness of the pes cross-axis (metatarsal-phalangeal joint row I–IV), and small but definite development of a pad at the position of the metatarsal-phalangeal joint of pes digit V.

Chirotherium barthi Kaup, 1835

Chirotherium majus Sickler, 1836.
Chirotherium gallicum (Bornemann MS.) Willruth, 1917.
Chirotherium barthi Kaup [in part], Soergel, 1925.
Chirotherium vorbachi Kirchner, 1927.

Type.—Not designated by Kaup; considered here to be best represented by Hessberg specimen at the Univ. Tübingen Geological Institute; photographed by Soergel (1925, fig. 1). The only Hessberg specimens which I have been able to locate and inspect in the United States are in the geological collections of Princeton University (nos. 11567, 2014). No. 2014 was obtained from Ward's Natural Science Establishment.

Referred specimens.—Univ. Calif. Mus. Pal. no. 37304, trackway of 5 consecutive steps; nos. 37305, 37317, 37318, 2 consecutive steps; no. 37306, 4 consecutive steps; nos. 37315, 37778–80, isolated sets of manus and pes impressions; Mus. Northern Arizona nos. 733/G2.2612, 2 consecutive steps, G2.2127, 3 consecutive steps.

Horizon and locality.—Upper Moenkopi southwest of Cameron, Arizona, U.C.M.P. loc. V3856, V4204.

Diagnosis.—Trackways of large chirotheriid with narrow pattern, pace angulation 170 degrees, but with relatively short stride, ratio of stride to pes length 5 to 1, manus turned out more than pes; pes digit group I–IV relatively long, not short and broad as in other large chirotheriids; pes shows moderate development of specialized pads which are more or less localized under individual digital joints, large circular pad covers the base of digit II and III; digit IV shorter than III and equal to II in length; digit V with large rounded pad centering about the position of the metatarsal-phalangeal joint; maximum pes length below 25 cm.; claws triangular in outline; pes digit V sometimes elongated posteriorly by broad metatarsal ridge.

Discussion

This original and best-known species is based on numerous trackways from the German Bunter of Hessberg near Hildburghausen. Study of American and European material indicates that the giant pes impressions which have been included in the species by European authors belong elsewhere. Such specimens are shown by Soergel in his figures 7, 31, 39, and 58. Certainly the pes shown in his figure 31 is not *C. barthi* and is most closely related to small manus chirotheriids such as *C. marshalli* from the Moenkopi. A similar pes associated with relatively small manus impressions from the German Bunther is called *C. barthi* var. *herculis* by Lilienstern (1939).

The species is represented in America by excellent material from the middle of the Upper Moenkopi southwest of Cameron. A series of sandstone slabs found just west of the stone quarry six miles south of Cameron contains three trackways of three different individuals (fig. 24). The largest and best, no. 37306, is described in detail. Isolated impressions of three individuals were found in a roadcut on the Flagstaff–Cameron highway east of the stone quarry. These are associated with the giant *Chirotherium rex*. In addition, isolated sets of footprints were found at V4204, several miles northwest of the quarry. One set, which is associated with the tiny trackway of *C. cameronensis*, reveals unusual detail of the pedal anatomy.

The University of California collection is believed to be fully representative for the species *C. barthi*. Several trackways known to be in collections at Grand Canyon National Park and at Cameron have been investigated (see p. 303). Major L. F. Brady, of the Museum of Northern Arizona, has kindly supplied a photograph of two consecutive steps found at the stone quarry, in about 1935 (pl. 39, *A*). This specimen is not the one figured by him (Brady, 1935). Measurements of Brady's specimen given here are based on a metric scale kindly added to the photograph by the museum director, Dr. H. S. Colton.

The footprints assigned to the species as described here have a wide range in size. The smallest pes is about one half the size of the largest one: 13.5 by 7.5 cm. compared with 24 by 19.5 cm. The wide range in size is attributed to age differences of the animals which made the tracks because the two extremes together with intermediate sizes occur together on the same surface and except for size are more or less alike. A similar range in size has already been described for trackways of *C. diabloensis* and *C. minus*. Despite the wide range in size, the species *C. barthi* as described here excludes giant footprints which in Europe are generally included either in the species or in a *C. barthi* "group." Because of the confused status of the species in Europe the American material is fully described.

Measurements of available specimens are assembled in tables 10 and 11. As can be expected, the variability of impression contributes to seeming inconsistencies, especially in digital length.

No. 37306

The trackway consists of 4 consecutive steps preserved as a cast on the under surface of a series of articulated slabs (fig. 24, *A*). The original surface cracked before and after the tracks were made; distortion of dimensions were accordingly discounted in the measurements.

The large animal which made the trackway walked straight across the surface with uniform stride, leaving no tail mark. Although fairly well impressed, the footprints are obscured in some critical places by a network of large and small cracks. The set of footprints shown in figure 25, *A*, is the best impressed and the least distorted of the 4 sets. However, the tips of pes digits II and III are cut by a wide crack which increases the overall length between 0.7 and 1.0 cm., and manus digits III and IV are distorted laterally by a small oblique crack.

The pace angulation and stride are relatively large, 170 degrees and 127 cm., respectively. The stride is 5.7 times the pes length. The pes impressions overlap the midline appreciably; digit II regularly falls directly over it. The manus by contrast does not overlap but nearly touches upon the midline. Unlike that of other chirotheriids, the pes is turned in more than the manus (10 degrees compared with 35). In fact, the manus is rotated so far from the midline that the tip of digit V is directed slightly backward. The manus occurs just in front of the pes and the transverse impression of manus digit V appears to "cross the T" with pes digit III.

The overall size of manus and pes is 12 cm. long by 10 wide and 22.5 long

TABLE 10

TRACKWAY MEASUREMENTS OF CHIROTHERIUM BARTHI

Measurements		No. 37304 (5 steps)	No. 37305 (2 steps)	No. 37306 (4 steps)	No. 37315	No. 37317 (2 steps)	No. 37318 (2 steps)	No. 37779	No. 37778	No. 37780	Mus. North. Ariz. no. G2.2612[a]
Stride, in cm.		74 74 75		128 127 ..	.. .. ..	.. .. ..	.. .. ..	.. .. ..	.. .. ..	.. .. ..	.. .. ..
Pace, in cm.		37 38 38 37	(52)[a]	65 63 64 ..	.. ..	(59)	59	.. ..	.. ..	52	48 .. .. ..
Pace angulation (in degrees)		167 168 165	.. .. ..	.. 170 169	.. .. ..	.. .. ..	.. .. ..	.. .. ..	.. .. ..	.. .. ..	.. (170) ..
Relation to midline	Pes	II on or over m-line	..	II on m-line	..	..	..	..	..	..	II on m-line
	Manus	II on, or nearly on m-line	..	I touches or nearly so	..	..	..	..	..	..	II on m-line

Divarication of foot from midline (III) (in degrees): Pes	7	..	9	..	..	12	..	..	..	11
	5	..	9	..	..	..	..	..	..	17
	0	..	10	..	..	..	..	..	..	..
	17	..	..	..	..	..	..	..	..	..
	0	..	..	..	..	..	..	..	..	..
Manus	30	..	32	..	..	35	diff. between m. and p. 10 to 15	..	..	25
	(19)	..	39	..	..	..		..	..	24
	16	..	33	..	..	..		..	..	..
	13	..	..	..	..	..		..	..	..
Pes, in cm.:										
Length	13.5	(16)	22.5	23	..	24	24 (27[b])	22.5	..	19
Width	7.5–8	11.5	17.0	16	..	16	19.5	16.5	..	14
Manus, in cm.:										
Length	5.5	..	12.0	10.3	11.5	..	13.5	..	6	10
Width	6.0	..	10.0	10.0	10.0	..	12.5	..	(5.5)	9
Pes length, in cm.	(9.0)	(10.5)	13.0	14.0	..	16.5	17	16.5	8.5	..
Pes width, in cm.	5.5	(7)	10.5	9.5	..	10.5	12	9.5	(5.5)	..
Divarication, I–IV, in degrees	(30)	35	40	35	..	33	45	32	..	30
Manus length, in cm.	(3.5)	..	7.0	(7.5)	7.0	..	8.5	..	4	..
Manus width, in cm.	5.2	..	9.5	9.0	8.5	..	11	..	4.5	..
Divarication, I–IV, in degrees	75	..	(90)	65	60	..	60	..	..	..

[a] Figures in parentheses are estimated.
[b] Includes metatarsal ridge.
[c] Measurements from photograph.

TABLE 11

LENGTH OF DIGITS IN *Chirotherium barthi*
(in centimeters)

Measurements		No. 37304	No. 37305	No. 37306	No. 37315	No. 37317	No. 37318	No. 37779	No. 37778	No. 37780	Mus. North. Ariz. no. G2.2612[c]
Manus	I	2.0	...	3.5	(3.0)	3.0	...	5.0	...	...	3.5
	II	3.5	...	5.5	6.0	5.5	...	7.5	...	3.5	6.0
	III	...	...	6.0	6.5	6.5	...	8.0	...	4.0	7.0
	IV	...	...	5.5	5.5	5.0	...	7.0	...	3.0	5.0
	V	...	...	(5.0)	4.5	5.5	...	(6.0)	...	...	5.5
Pes	I	4	(5)[a]	8.5	7.5	...	8.0	10.5	8.5	4.5	7.0
	II	7	(9)	11.0	11.5	...	12.5	13.5	12.0	7.0	10.0
	III	8	(10)	13.0	13.5	15.0	15.0	15.5	15.0	8.0	12.0
	IV	7	(9)	11.5	12.0	12.0	...	13.0	14.0	...	10.5
	V	5	6.5	13.0	10.5	...	(11)	11[b]	10[b]	...	10.0

[a] Figures in parentheses are estimated.
[b] Excluding metatarsal ridge.
[c] From photograph.

by 17 wide, respectively—much larger than the smallest trackway (no. 37304) on the same surface but smaller than the largest specimen from the roadcut locality (no. 37779). Thick digital pads which obscure in part the phalangeal formula of the foot are well developed on both manus and pes.

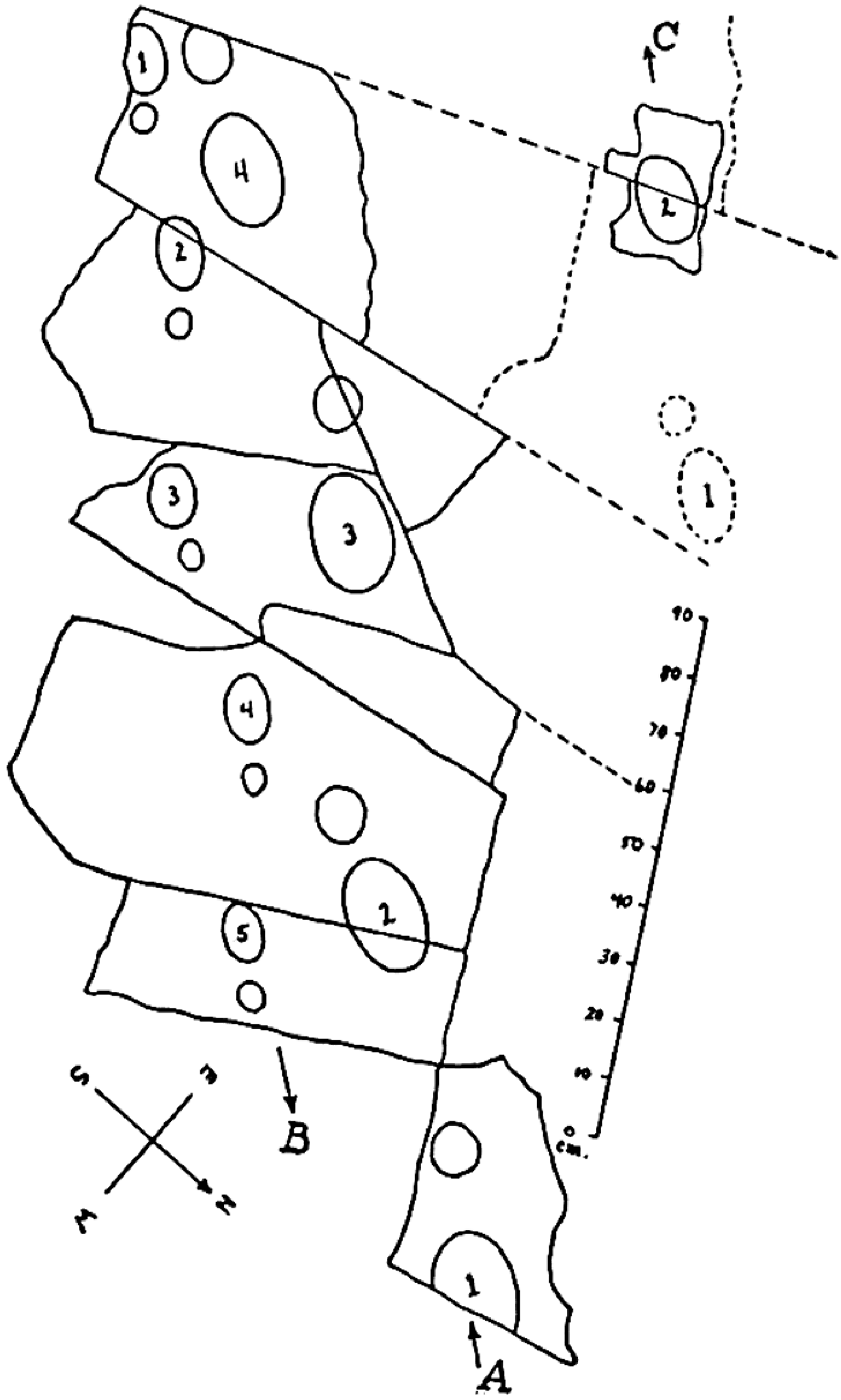

Fig. 24. Trackway pattern of three different individuals of *C. barthi* on a series of slabs from the Upper Moenkopi southwest of Cameron, loc. V3856: *A*, no. 37306 (fig. 25, *A*); *B*, no. 37304; *C*, no. 37305 (fig. 25, *C*).

Manus.—The proportions of the manus resemble those of *C. diabloensis*, a much smaller chirotheriid, and bear approximately the same relation to the pes, that is, the manus is not reduced in size as it clearly is in *C. coltoni*, described later. The impression of digit V is separate from the digit group I–IV and not bunched with it as in more specialized forms.

The digits are thickly lenticular in outline, cabochon-like in contour, and with sharply rounded but not pointed ends. Digits I–IV appear to have short stubby claws of broadly triangular outline in some impressions, but their presence is usually obscure. Their identity seems to be largely lost in the thick homogeneous digital pads which underlie them. The outline and contour of

the digits show no sign of knobbed enlargements or transverse ridges as in the pes.

The impression of digit I and V is often obscure, particularly the proximal part. The length of digit V increases with the depth of impression, and its proximal border never shows any definite outline because it passes smoothly into the recording surface. Digit V seems to have been independent of group I–IV, and is always inclined to the plane of the recording surface. Digits I–IV diverge from each other a total of 57–90 degrees.

Pes.—The pes is more deeply impressed than the manus. Digits I–IV are relatively widespread, 40 degrees total divarication, as is also true of the manus. Digit IV is shorter than III but as long as II so does not approach the extreme shortness of *C. marshalli*. Short, heavy claws broadly triangular in outline are present on digits I–IV. The tips are blunted, probably from wear.

As shown in figure 25, *A*, the contours of the digit impressions show swellings and faint transverse divisions of the thick digital pads. The most characteristic feature of the pes, and this is true of all specimens assigned to this species, is found in the proximal region of digits II and III. The bases of these digits, separate in most species, here lose their identity in a single large metatarsal-phalangeal pad.

Also the central part of the posterior border of digit group I–IV is strongly indented and faintly impressed. These facts suggest that the row of metatarsal-phalangeal joints (I–IV) was strongly arched transversely. In any event the community of the basal portion of digit II and III contrasts strongly with the definite separation found in the contemporary giant, *C. rex*, and in the small primitive forms.

Digit I is formed like a slender pear, the claw being the stem. The position of the two phalanges is clearly indicated by the contours. Digit II, distal to the communal pad with III, shows a wide enlargement (4 cm.) in the region of the first phalangeal joint, followed by a much narrower one in the region of the terminal (second phalangeal) joint. The central one third of digit III (the region of the first phalangeal joint?) is faintly impressed and secondary in importance to the distal one third, which is wider and shows a thick pad 4 cm. wide, underlying and obscuring the position of the second and third phalangeal joints. Digit IV shows three or possibly four enlargements very faintly, but they are of uniform width and not so wide as in II and III. The metatarsal-phalangeal pad of digit IV is separate from the communal pad of II and III and is connected to the impression of V by a low ridge formed by the sole underlying the fourth metatarsal.

Pes digit V is so fully impressed in step 2 (fig. 25, *A*) that its dimensions are much larger than usual. The median border of the impression overlaps the extended long axis of digit I, an unusual expansion. Unfortunately, the impression is partly missing in step 1, obscured by cracks in step 3, and faintly impressed in 4. In step 2, digit V is complicated by a double impression of the distal portion. As a result of these deficiencies, digit V of the trackway fails to provide a clear picture of the typcial impression, which consists of a large rounded base separated from a relatively slender distal portion by a faint linear

constriction. These characters are clearly shown in all other specimens assigned to the species, particularly the specimen shown in figure 25, *B*.

It is easy to overemphasize the rather large variations found in the impression of the chirotheriid fifth digit. I believe that most of the variation can be

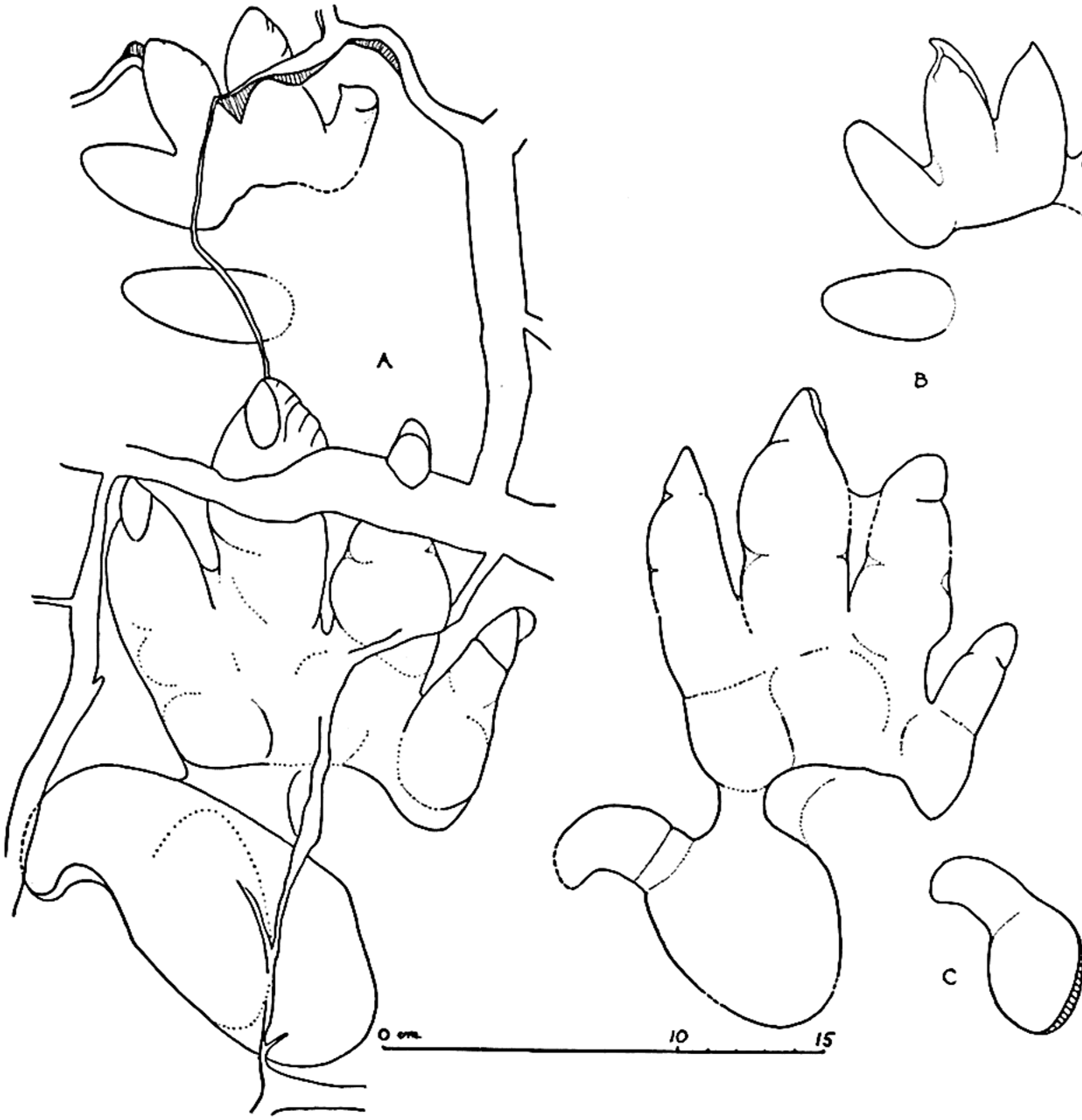

Fig. 25. ***Chirotherium barthi: A,*** **set of footprints from trackway no. 37306, step 2 (fig. 24), in which crack system has lengthened pes digits II and III and distorted manus digit II; *B,* isolated set of footprints showing excellent detail of the plantar surface (pl. 40); *C,* sharply incised pes digit V of a small individual, trackway no. 37305 (fig. 24, *C*).**

attributed to differences in depth of impression, and in speed. The two smaller trackways from the same surface seem to suggest also that a smaller, lighter animal of the same species will have somewhat less development of certain callosities, such as that at the base of pes digit V.

The pes of trackway no. 37305 is about two thirds the size of that in trackway no. 37306 and similar in character, except that the basal pad of digit V is relatively smaller in area and more precisely limited proximally (fig. 25, *C*). This is true also for the pes of the still smaller trackway no. 37304, which is

similar to no. 37306 in every respect save size and character of pes digit V. Neither of the smaller trackways is as deeply impressed as the type and therein may lie the fundamental reason for the differences in digit V. In any event the clearly impressed pes digit V of the smaller trackways is more closely comparable to the better impressions of isolated footprints from other trackway surfaces.

Until such time as better material may prove otherwise, it is best to regard the smaller trackways as representing smaller, possibly younger individuals of *C. barthi.*

No. 37315 (fig. 25, *B*, pl. 40, *A*)

A slab containing the cast impressions of a manus and pes was found in locality V 4204, several miles northwest of the stone quarry at about the same level. The impressions are very clear and lack the distortion common to deeper footprints; therefore, the specimen can be used to verify characters of no. 37306 which are obscured or distorted by extramorphologic characters.

Manus.—The manus is impressed most deeply on the outside and digit I barely touched the ground. This condition, together with the turned-out position to the manus, seems to be characteristic of *C. barthi.*

The homogeneous nature of the digital pads is incontrovertibly displayed. There is no suggestion of enlargement or transverse creases in the pads although the detail of skin sculpture is apparent on each. The even larger manus of *C. rex* is similar in this respect and strengthens the premise that, contrary to Soergel's belief, the large chirotheriids were completely quadrupedal as adults. A manus not habitually used for walking would surely be flexible and the flexibility would probably be suggested by transverse divisions of the digital pads.

Pes.—The large, central metatarsal pad which covers the base of digits II and III extends forward so far that the hypex between the two digits is noticeably forward of the hypex between I and II and between III and IV.

The marked enlargement at the first phalangeal joint of digit II and the large digital pad covering the distal one third of III are clearly shown to be real, not an accident of distortion as in no. 37306. The obscure impression of these digits just anterior to the communal metatarsal pad is further evidence of a strong transverse arch of the row of metatarsal-pahlangeal joints (I–IV) perpendicular to the long axis of the metatarsal bundle.

The outline of digit IV proves that it actually is relatively slender. The tendency of the walking foot to emphasize its impression probably accounts for the usual robust contours of digit IV in the average trackway.

Digit V shows the gourd-shaped outline so characteristic of good pes impressions of the species. The enlarged base passes proximally into the recording surface smoothly and with no indication of change of contour. Distally it is concisely limited, particularly in its outer border. The slender distal half of V seems to sprout from the massive base and curve backward like the neck of a gourd. The neck is separated from the base by a clearly defined furrow or crease. Distally 1 cm. from the major crease is another broader furrow. The presence of the transverse divisions indicates flexibility between the slender

neck and massive base. This does not mean that a skeletal joint or joints overlay the furrows. Feet of living animals show that such furrows are mesarthral.

The claws are especially well depicted in the long pes digits II–IV. These digits are most often distorted by movement of the foot. The claw on digit II and III is more massive than on I and IV. All are broadly triangular in outline and separated from the digital pad by a transverse furrow. Digit V is not clawed in either manus or pes. Manus digit IV, in common with other specimens, seems to lack a claw.

Detail of the skin surface is well shown on both manus and pes. Some indication of it is present on all parts of the impressions except, of course, the claw impressions. The sharpest detail is on the base of digit V of manus and pes. These areas are shown in natural size in plate 40. The beadlike scales are rounded or hexagonal and appear to be of uniform size on manus and pes. The maximum diameter is about 2 mm. and no difference in size from one area to another on the plantar surface is noticeable. Certainly there is no differentiation such as that found on a giant chirotheriid from Utah (pl. 41).

No. 35836

A large slab from the road cut south of Cameron (no. 35836, V3856) contains three sizes of footprints of *C. barthi* (pl. 43). The isolated pes impression, no. 37778, is the same size as that in trackway no. 37306. It is exceeded in size by the pes of a large set of footprints, no. 37779, heading in the opposite direction (see table 10 for comparative measurement). Both isolated specimens show essentially the same characters as those described above except that the impression of pes digit V is continued backward by a broad metatarsal ridge. The elongation is not a regular feature of the impression. The support for the foot is localized in the rounded metatarsal pad. This differs importantly from the "flat-footed," more completely plantigrade species, *C. rex*, occurring on the same surface.

The manus of the largest set of impressions, no. 37779, is one of the largest known for *C. barthi* but is nevertheless dwarfed in comparison with the huge manus of *C. rex* just behind it. Its general appearance is similar to no. 37306, but the digits are relatively broader, which is a further suggestion that with increase of body mass in *C. barthi* the digits become slightly more massive, at least so far as the digital pads are concerned. Digit III at the hypex is 2.8 cm. wide. The manus, as in *C. rex* appears to be almost hooflike, further strengthening the premise that the large chirotheriids are completely quadrupedal.

The single set of small footprints, no. 37780, is about the size of the smallest footprints occurring with no. 37306 and is similar in character. In part it is more clearly impressed. Again it could be argued that this small form represents another species, but for reasons already stated it is regarded as the young stage of *C. barthi*.

The tail

A tail mark was found associated with two consecutive steps comparable in size and character to no. 37306 (no. 37317, V4204, pl. 40, *B*). The ridge formed by the tail crosses pes digit I, passes the median border of II, crosses manus

digit II, and curves broadly forward and inward, passing 7 cm. medial to the base of digit V of the next succeeding pes, a distance of 56 cm. It continues strongly to the edge of the slab, so it must have been still longer. The ridge is rounded in cross section and .6 cm. wide (max.). It is discontinuous by reason of an irregular recording surface.

The tail mark has about the same relation to the two consecutive steps as in the trackway of *C. diabloensis*. Also it is correspondingly large so there is little doubt that it belongs with the designated trackway. This tail mark is the only example known for *C. barthi*. The rounded cross section represents the relatively sharp keel of a long balancing tail which occasionally dragged the ground. An even larger keel mark is shown on the trackway surface from the road-cut locality, but it cannot be directly associated with the large footprints near it.

Relationships

The trackways described here undoubtedly represent the American equivalent of the European *Chirotherium barthi* Kaup as originally described from the trackways from Hessberg near Hildburghausen. The American specimens might be given separate status by reason of wide geographic separation and by reason of the confused taxonomy of the species in Europe. However, no clear differentiation can be made here on the basis of the trackway characters alone. The American trackways are described fully in an effort to define the species more closely than it is done in Europe, where giant forms are commonly included.

Trackways of *C. barthi* represent a large, heavy-footed chirotheriid with a narrow trackway pattern but with a ratio of stride to pes length not much larger than primitive *C. diabloensis*. The digits have thickened pads which in pes I–IV partly obscure the phalangeal formula and in the manus completely obscure it. The development of pads on the pes is less than found in the giant and in the small-manus species of the Moenkopi. The manus is relatively shorter than in primitive species but longer than in small-manus species, and digit V retained its independence of group I–IV. In large individuals the manus appears almost hooflike, as if specialized solely for a quadrupedal gait. The pes is characterized by having digit IV only slightly longer or equal to II but not shorter than II. Digit group I–IV is relatively long compared with other large chirotheriids. The base of digits II and III is covered by a large communal pad which, together with a strong indentation of the posterior border of digit group I–IV, indicates a definite transverse arch in the row of metatarsal-phalangeal joints I–IV. Pes digit V has a large rounded pad centering about the position of the metatarsal-phalangeal joint. It is intermediate in development between the small pad of *C. minus* and the elongate or ovoid pad of certain other species.

Chirotherium moquiensis n. sp.

Type.—Univ. Calif. Mus. Pal. no. 37345, cast of right manus impression; no. 37784, cast of left pes impression, fig. 26, pl. 42, *D*.

Horizon and locality.—Lower Moenkopi of Moqui Wash, several miles west of Winslow, Arizona; U.C.M.P. loc. V4126.

Diagnosis.—The footprints represent a giant chirotheriid of bulky foot structure; pes length 30 cm.; digits heavily padded, digits II–IV showing proximal and distal pads; pes digit V massive, with massive, elongate, metatarsal pad and strongly developed phalangeal portion, pes digit IV shorter than III and subequal to II, and with weakly impressed base; manus relatively large and wide, with digit V often weakly impressed; claws triangular in outline.

Discussion

The two isolated footprints upon which the new species is based came from a trackway surface occurring about halfway between bottom and top of a butte in the northeast corner of section 24, Moqui Wash locality map. A geologic section taken through the butte (sec. 6) indicates by correlation with 9 other sections that the trackway level is at least 65 feet above the base of the Moenkopi and approximately 20 feet below the middle gypsum zone.

The trackway surface outcrops around the entire semicircular periphery of the butte so it must be extensive. The slabs are thick, and considerable excavation would be necessary to collect the large trackway even it if paralleled the outcrop. The trackway to which the footprints belonged could not be found and only a few slabs which had slumped from the outcrop were collected. The manus and pes impressions were found close together but not otherwise associated. They are about the right size to have been made by a single individual, although the manus is relatively large. Similar proportions were noted in a trackway found a mile southwest of locality V4126. The footprints are so near the edge of their respective slabs that the manus lacks the tip of digit III and IV, the pes lacks the tip of digit III and V.

The importance of this meager material lies in the proof given of the existence in the Lower Moenkopi of a giant species of *Chirotherium*. Furthermore it proves to be closely related to another giant species from the Upper Moenkopi, *C. rex*.

Measurements are included in the description of *C. rex*.

Manus (*no. 37345*).—The impression is definitely that of a large manus but it is not very clear. Digit V is obscure and weathering has erased detail from the strongly impressed digit group I–IV. Judging from measurements of group I–IV, the manus is nearly as large as that of *C. rex* and generally similar in character. It is slightly less broad and the digits are not so thick.

Pes (*no. 37784*).—The pes impression is clear enough to show the beaded surface of the skin over much of the surface. Strong lateral pressure exerted on the foot pushed the lateral border of digits I–III over the medial border of the neighboring digit. The tips of II–IV were distorted by retraction of the foot so their character is obscured. A double impression of the lateral border of digit V was caused by a shifting of the heel. The skin granules on the double impression show no sideslipping, so the heel must have been raised slightly as it shifted. The lateral movement of digits I–IV and the medial movement of the heel apparently took place simultaneously as the foot rotated in the impression.

The pes is immediately distinguished from other species, except *C. rex*, by two characters: (1) digits I–IV are separated from each other by a furrow which

extends proximally from the hypex across the metatarsal-phalangeal axis to the proximal border of the digit group. (2) The proximal border is formed by the contours of the nearly separate digit impressions; digits II and III, particularly II, extend proximally beyond I and IV. Thus the familiar indentation of the proximal border of digit group I–IV of other species is reversed. The

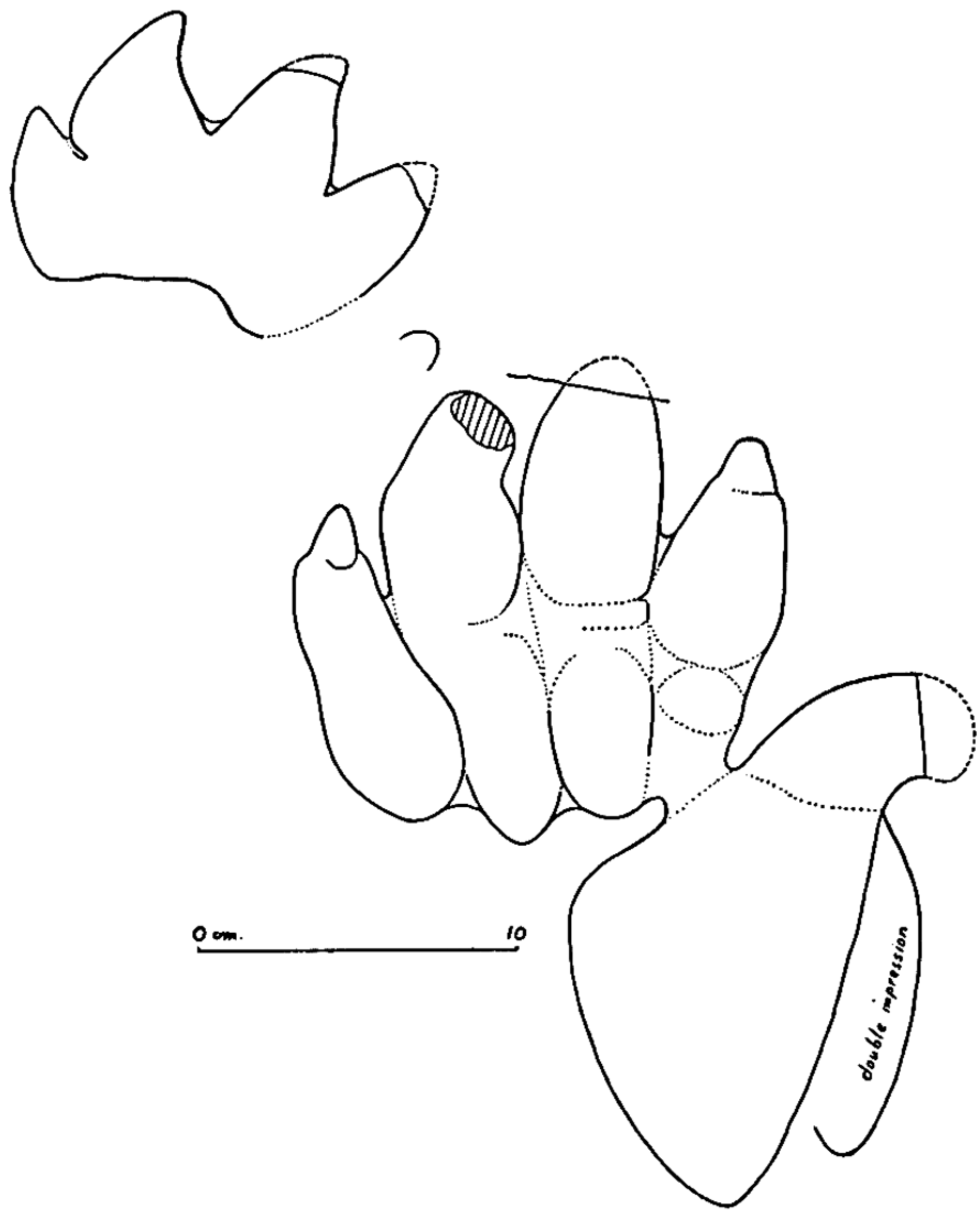

Fig. 26. *Chirotherium moquiensis* (type); disassociated manus and pes impressions from the same trackway surface in the Lower Moenkopi of Moqui Wash, loc. V4126.

proximal elongation of the impression of II and III cannot represent a corresponding proximal displacement of the metatarsal-phalangeal joint. A backward curve of the joint row is unknown among tetrapods. The explanation probably lies in the nearly prone metatarsals of a very "flat" foot. The row of metatarsal-phalangeal joints certainly lacked the transverse arch of *C. barthi*. The contours of the proximal ends of digits II–IV give no indication of the exact position of the overlying joints.

Digits II–IV have large pads on their distal halves. A median area of flexure separates the distal from single proximal pads which are progressively smaller from II to IV. Digits I–IV are slightly flexed midway of their length.

Digit III is relatively short in spite of the proximal elongation and it is only

slightly longer than II. Both are much longer than IV. This proportion of toe length is not found elsewhere except in *C. rex*. The base of digit IV is connected to V by a metatarsal ridge.

Digit V is clearly impressed. It is characterized by a massive enlargement of the metatarsal pad which extends proximally to a concisely impressed heel, the proximal end of the metatarsus. The flat metatarsal pad is broad, exclusive of the double impression, and long (9 by 14 cm.), and is roughly triangular in outline in contrast with the ovoid pad of *C. marshalli*. The contours of the pad are unbroken by a "high" in the distal region indicating that the whole pad habitually supported nearly half the weight borne by the pes. The phalangeal part of digit V is larger than in other chirotheriids except possibly *C. rex*. It is set off from the metatarsal pad by a shallow furrow.

The general massiveness of the pes masks the fact that the phalangeal segment of digit V extends relatively far forward. The whole appearance of digit V suggests the role of principal weight carrier of the foot. The relative development of digit V is greater than in any known species except perhaps *C. rex*.

The nature of the claws is completely obscured in all digits but I. Here the claw outline is definitely triangular, not spatulate as in the corresponding digit of *C. rex*.

The skin has a coarser texture than that of *C. barthi*.

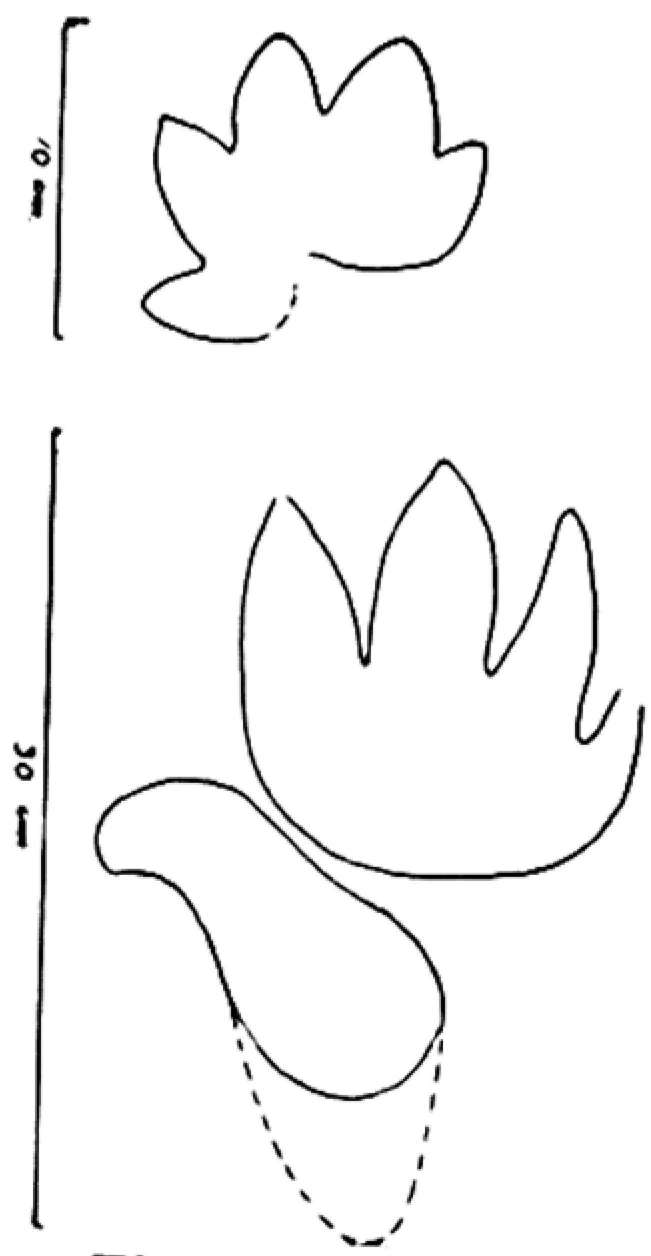

Fig. 27. Large chirotheriid from the Lower Moenkopi of Moqui Wash; probably represents *Chirotherium moquiensis*. Trackway not collected; rough sketch from author's notes, 1941, p. 231.

Additional specimens of *Chirotherium moquiensis*

Several large and fairly clear chirotheriid trackways were discovered on the underside of a massive layer of sandstone in Moqui Wash (Moqui Wash loc. map, NW. corner of section 25 at "x"). Unfortunately the trackways have not been collected; available information consists of a few measurements and rough sketches (author's field notes, 1941, p. 231, 1946, p. 457). The level is slightly higher in the Lower Moenkopi than the type of *C. moquiensis* but still well below the middle gypsum zone. The trackways generally parallel the outcrop in a north–south direction and extend for a distance of about 90 feet.

The stride is 140 cm. and the ratio of stride to pes length is about 5 to 1. The pace angulation for one series of 3 consecutive steps is 140 degrees. The position of the manus is more median to the pes than in *C. barthi*, a character also noted in *C. rex*. Manus digit V usually is lightly impressed and therefore appears to be small, as in the type specimen. Overall dimensions of the manus and pes (fig. 27) are: 10 cm. long by 17.5 wide, and 30 long by 20 wide, respectively. Manus digit group I–IV measures 16 cm. long by 20 wide. Pes digit V is large and projects well forward and outward. The basal pad of V is relatively large and long; the phalangeal part is massive and unreduced. The claws on the pes are triangular in outline, not spatulate.

The 140-cm. stride is about one sixth longer than any recorded for *C. barthi*.

The character of pes digit V, the relative length of pes II–IV, the convex outline of the posterior border of pes digit group I–IV, and the shape of the claws are also characteristic of the isolated footprint described as *C. moquiensis*. It will be recalled that the manus associated with the type pes is relatively large and broad and has a relatively small digit V. Observations of the uncollected trackways indicate a manus of similar character.

A trackway of similar but smaller footprints was discovered on the underside of another thick sandstone southeast of the Winslow–Payson road, 9 miles southwest of Winslow (author's field notes, 1941, p. 232). The trackway was not collected. The stride was approximately 130 cm.

Chirotherium cf. *moquiensis*
(pl. 41)

Footprints of a giant chirotheriid discovered in the upper Moenkopi near Rockville, Utah, at the mouth of Zion Canyon (V4603), represent the first known occurrence of the genus in Utah. Two left pedes, one deeply impressed with the distal part of digit I broken off (no. 38028) and one lightly impressed with the greater part of digit V broken off (no. 38029), occur on one slab close together and pointing in the same general direction. On another slab from the same level but not connected with the first occurs a poorly preserved left manus. Preservation in perfect detail of the scaly plantar surface is offset by weathering which has destroyed the distal parts of the digits of the deeply impressed pes and all the anterior part of the manus except digit IV. Also smaller animals skidded about on the original surface and obscured some detail.

Pes (no. 38028)

The pes is 34 cm. long by at least 21 cm. wide overall and is impressed to the depth of 5 cm. in the region of the fifth digit. The whole of the metatarsal region is impressed, giving the footprint a maximum width of 18 cm. across the middle of digit V. The fifth digit itself is 21 cm. long from tip to sharply incised heel.

Digit group I–IV is about as broad as long and digit IV is shorter than II but not excessively so. The metatarsal-phalangeal axis is indistinctly impressed but shallow furrows run across it separating I from II and II from III. The base of IV is "squeezed out" between III and V. Digit V is massive, elongate, and the phalangeal part is massive. The claws on the first four digits were apparently triangular although the impressions are distorted by movement of the emplacing foot. The second pes impression clearly shows narrowly triangular claws on digits I to II at least. Contours of digits III and IV show differentiated pads similar to the type of *C. moquiensis*.

Impression of the scaly plantar surface is perfect on several areas of the footprint. The scales are usually polygonal or hexagonal and range in diameter from 2 to 5 mm. The largest scales which occur on the metatarsal region and on the metatarsal-phalangeal axis are flattened. The smallest scales are rounded or granular and occur on the lateral border of the distal part of digit IV. This is the first chirotheriid to show differentiated scales on the plantar surface.

The pes twisted or pivoted inward as it emplaced so that the lateral borders of digits II–IV slope toward the mid-line from the recording surface and the lateral border of V slopes in the opposite direction. The lateral borders are scalloped by evenly spaced vertical furrows which undoubtedly represent the impressions of fringe scales comparable to those of recent lizards. The fringe scales were appreciably larger than the plantar scales, having a maximum width of 8 mm. on digit V and about 6–7 mm. on digits II–IV.

Pes (no. 38029)

This pes is impressed to the depth of 2.5 cm. in the region of digit I, but it is so lightly impressed laterally that digits IV and V show only the shallowest of impressions. Digits I–III at least have long narrowly triangular claws, that on II measuring 3 cm. long by 1.5 cm. wide at the base. The scaly plantar surface is perfectly impressed on part of the metatarsal area and on part of digit III. Both pes impressions undoubtedly represent the same or similar individuals, the differences arising from different modes of impression.

Manus (no. 38030)

Only the close association with the pes impressions justifies identifying this specimen as that of a manus. Most of the anterior part of the manus, which is deeply impressed (4 cm.), is destroyed by weathering. There remains the impression of digit IV and of the posterior border of digit group I–IV. On these areas the scaly plantar surface is clearly shown. Individual scales are 3–4 mm. in diameter and rounded in contour. The maximum width across digits I–IV is 16 cm., commensurate with the relative size of the giant pes. There is no indication of a fifth digit impression.

The giant chirotheriid represented by these three footprints definitely belongs to the large-manus group of the Chirotheriidae. It shares with *Chirotherium moquiensis* and *C. rex.* fundamental characters which at first glance are obscured by different modes of impressions in known specimens. The pes is of giant size, digit IV is shorter than II but not much and its base is nearly "squeezed out" between III and V, shallow furrows cross the metatarsal-phalangeal axis between digits I and II and between II and III, digit V is massive, as is the unreduced phalangeal part which extends obliquely far forward nearly to the middle of digit IV, and the metatarsal pad of V is massively elongate. The manus is also relatively large and broad.

In size this chirotheriid equals *Chirotherium rex* but has claws of sharply triangular outline in contrast with the broad spatulate ones of the latter. The essential difference between the Utah chirotheriid and the type of *C. moquiensis* is hard to determine because of the markedly different mode of impression. The Utah chirotheriid is appreciably larger but details of digit group I–IV, such as the differentiation of digital pads and the "squeezing out" of the base of digit IV, are common to both. The deeply impressed fifth digit at first appears to have an ovoid pad because of the greater area of the metatarsal region impressed, but contours of the pad suggest that in light impression the angular outline of the type might be produced. Unfortunately the known specimens

of *C. moquiensis* and *C. rex* show hardly any scalation so the range of plantar scale size cannot be compared.

The stratigraphic position of the Utah chirotheriid is definitely the upper part of the Moenkopi, but the question arises just how this level in a 1,500-foot section correlates with the track levels of a much thinner 300-foot section in the distant Little Colorado Valley. The fact that the Utah chirotheriid occurs only 60 feet below the Shinarump and above a gypsum zone as do the track levels near Cameron suggests a general correlation. This means then that a giant chirotheriid as represented by *C. moquiensis* of the Lower Moenkopi still existed in late Moenkopi time.

Relationships

C. moquiensis represents a very large, awkward-footed chirotheriid with claws more or less triangular in outline. Good footprints of a giant form, *C. rex*, with the same general type of foot but possessing heavy spatulate claws, occur in the Upper Moenkopi of Cameron. Comparison of the two related forms is made following a description of the second species.

Chirotherium rex n. sp.

Type.—Univ. Calif. Mus. Pal. no. 37782, isolated set of manus and pes impressions lacking pes digit V, pl. 43.

Referred specimens.—U.C.M.P. nos. 37783–37785, isolated impressions of manus and pes occurring on the same slab as the type, and of about the same size; no. 37787, fragment of pes.

Horizon and locality.—Upper Moenkopi southwest of Cameron, Arizona; U.C.M.P. loc. V3856; possibly Lower Moenkopi, V4145.

Diagnosis.—Footprints of a giant chirotheriid somewhat larger than *C. moquiensis;* pes length over 33 cm., but otherwise similar to *C. moquiensis*, except for claw impressions on pes digits I–IV which are rounded or spatulate-like instead of triangular; manus is hooflike with wide, stubby digits and with a strong claw on digit V.

Discussion

The trackway surface from which the slab shown in plate 43 was taken occurs in a road cut on the Flagstaff–Cameron highway 6 miles south of Cameron. Unfortunately the heavy overburden in the road cut prevented the collection of enough of the surface to show a full trackway of the large footprints. The right hand edge of the slab, as shown in the photograph, was all that was originally exposed.

The giant footprints described here as *C. rex* are all of a size so the description is based on their composite detail. Two sets of manus and pes impressions can be recognized. In each the respective position of manus and pes is normal for *Chirotherium*. The best set, no. 37782, is designated as the type. Detail of the individual footprints is clear and justifies description of a new species of chirotheriid which differs markedly from contemporaneous *C. barthi* as well as from other species with the possible exception of *C. moquiensis*. The associated footprints of a very large individual of *C. barthi* are dwarfed by comparison with the giant, *C. rex*.

Manus.—The manus has the same general plan as the large manus of *C.*

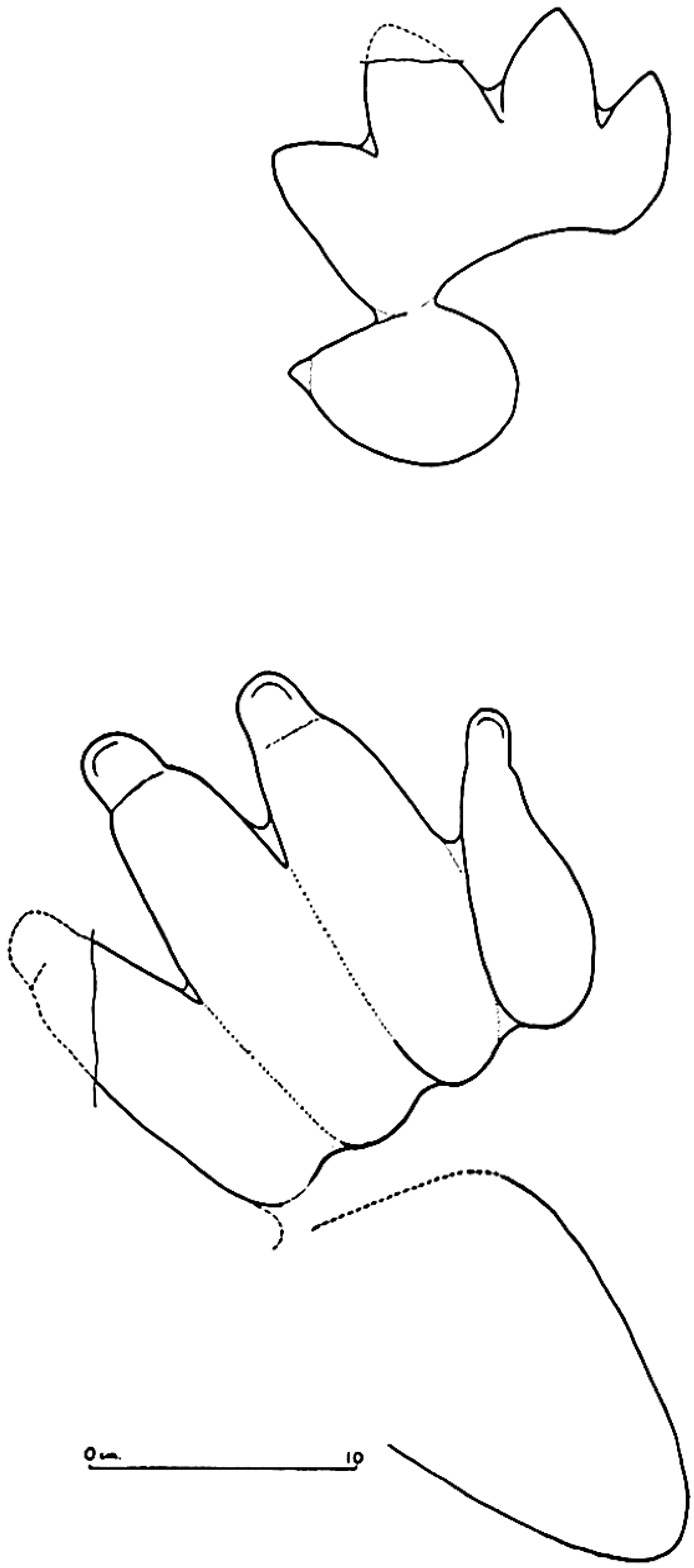

Fig. 28. *Chirotherium rex;* manus and pes, based on composite detail of footprints shown in pl. 43.

barthi. Closer comparison shows it is relatively broader and thicker-toed as well as being one fourth larger overall. Digit III, where it joins the others, is 4 cm. wide compared with 2.8 cm. Digit V, which is 4 cm. wide, is more ovoid in outline than in *C. barthi* and seems to be more closely appressed to digit group I–IV, but it probably had more independent movement than digit V in the manus of *C. marshalli*. Probably the closeness is due to the greater relative width of digits and not to a lack of independence of V seen in *C. marshalli*.

The identity of the claws in digits I–IV is obscure but the digit tips bear a general resemblance to those of *C. barthi*. Certainly there is no indication of spatulate claws such as are present on the pes. Of particular interest is the indication of a short claw of triangular outline on digit V. The tip, ordinarily rounded in other species, is extended 1 cm. into a broadly triangular point. The triangle is separated from the digital pad by a shallow furrow, best shown by no. 37785.

A homogeneous digital pad covered each digit so that the entire appearance of the manus suggests specialization for one purpose, namely, supporting heavy weight in a quadrupedal gait. Bipedalism as a habitual gait would seem out of the question for *C. rex*.

Pes.—The pes differs from all other species in having claws which are large and bluntly rounded or spatulate in outline. It differs from all species but *C. moquiensis* in having digits I–IV completely separated from each other by a shallow furrow running from the hypex back and across the metatarsal-phalangeal axis.

Digit group I–IV is about as broad at the base as it is long and hence is relatively short.

The proximal border of digit group I–IV is not arched forward nor is the metatarsal-phalangeal axis. The proximal border is formed by the contours of the nearly separate impressions of the digits. Digit II bulges the general line of the border much more than the others (no. 37782). The pes of *C. moquiensis*, a sharp-clawed relative from the Lower Moenkopi, shows this character of the proximal border more clearly.

Digit III is relatively short and is only slightly longer than II; both are longer than IV. All 4 digits are relatively massive and larger than in any species known in America or Europe.

The claws are so clearly impressed as to leave no doubt of their character. On digit I the claw impression is 3 cm. long by 2 wide at the base. It is broadly rounded but narrower overall than the others. On digits II–IV the claw is bluntly rounded and relatively broad, 3 cm. long by 2.5 wide. A hollow in the center of each claw impression clearly represents the position of the softer, less resistant core of the original structure. The outer shell of the claw apparently was very thick and strong. The claws are separated from the digital pads by a break in the contours of the digit impression.

The character of digit V is not clearly shown on the trackway surface from south of Cameron. The one full impression collected (no. 37784) is obscured in the critical region by at least three other foot impressions. However, the broad outline of a very large metatarsal pad is apparent in the confusion of impressions. It is similar, so far as it is impressed, to the equally massive metatarsal pad of *C. moquiensis*. It is not certain if additional footprints from the uncollected Cameron surface could add much detail considering the probable firmness of the original surface. The large plantar area of digit V distributed its load more widely than the less expanded digit V of *C. barthi*, which is itself rather shallowly impressed.

The footprints of *C. rex* are those of a very large, heavy animal which even if

bipedal in its youth was certainly purely quadrupedal as an adult. The manus is as big relative to the pes as in any species except *C. cameronensis* or *C. moquiensis*. The pes is more fully plantigrade than any other species save *C. moquiensis*. The pes seems particularly flat-footed and would seem to indicate that the reptile suffered from fallen arches. A transverse arch of the metatarsal-

TABLE 12

COMPARATIVE MEASUREMENTS OF *C. moquiensis*, *C. rex*, *C. barthi* (in centimeters)

Measurements		*C. moquiensis*, Nos. 37345 and 37784 (Lower Moenkopi)	*C.* cf. *moquiensis*, Nos. 38028–38030	*C. rex*. Nos. 37782–37785 (Upper Moenkopi)	*C. barthi*, No. 37779 (largest known specimen)
Manus, over-all	L	....	..	14.5	13.5
	W	....	..	15.5	12.5
Digit I–IV	L	(9.5)[a]	..	9.0	8.5
(max.)	W	13.5	16.0	14.5	11.0
III	L	(8.5)	..	8.0	....
(at hypex)	W	4.0	..	4.5	....
V	W	....	..	5.0	....
Pes, over-all	L	30.0 [28.5 + (1.5)]	34.0	33.+	24.0
	W	21.0 [19.5 + (1.5)]	21.0	(23.0)	19.5
Digit I–IV	L	16.0 [15.0 + (1.0)]	16.5	17.0	17.0
(max.)	W	15.5	17.0	21 (16.0 across claw tips of I–III)	....
(at base)	W	12.0	14.5	17.0	12.0
I–IV divarication (in degrees)		30	25	30–35	....
digit length (in cm.):					
I		10.5	10.5	11.0	10.5
II		15.0	15.0	16.0	....
III		15.5	16.0	15.0	15.5
IV		13.0	13.5	(12.0)	13.0
V		18.5	21.0	(19.+)	11.0
Claws		triangular	triangular	spatulate	triangular

[a] Figures in parentheses are estimated.

phalangeal axis, so well developed in *C. barthi*, seems to be lacking entirely. The basal pad of digit V apparently extended to the proximal end of the fifth metatarsal, where a more or less definite heel is indicated by the conciseness of the impression. Digit V supported nearly half the weight carried by the pes compared to a much smaller proportion for *C. barthi*.

The presence of *C. rex* in the Lower Moenkopi is indicated by a fragment of a very large pes impression from the subgypsum strata near Leupp (U.C.M.P. loc. V4145, specimen no. 37787). The tip of digit I and all of digits III–IV and V are missing from an otherwise excellent impression. Digit II is 15.5 cm. long and resembles that of *C. rex*. The claw dug into the recording surface leaving

a square-ended impression 2.2 cm. wide, evidence of a spatulate claw. Excellent detail of a coarsely beaded skin similar to that of *C. moquiensis* is present over most of the impression. This fragmentary evidence indicates that *C. rex* and *C. moquiensis* were more or less contemporaneous in early Moenkopi time.

Relationships

C. rex differs from the type of *C. moquiensis* by having rounded or spatulate claws on the pes rather than claws of triangular outline, and by having a strongly impressed manus digit V. Both species differ from other chirotheriids

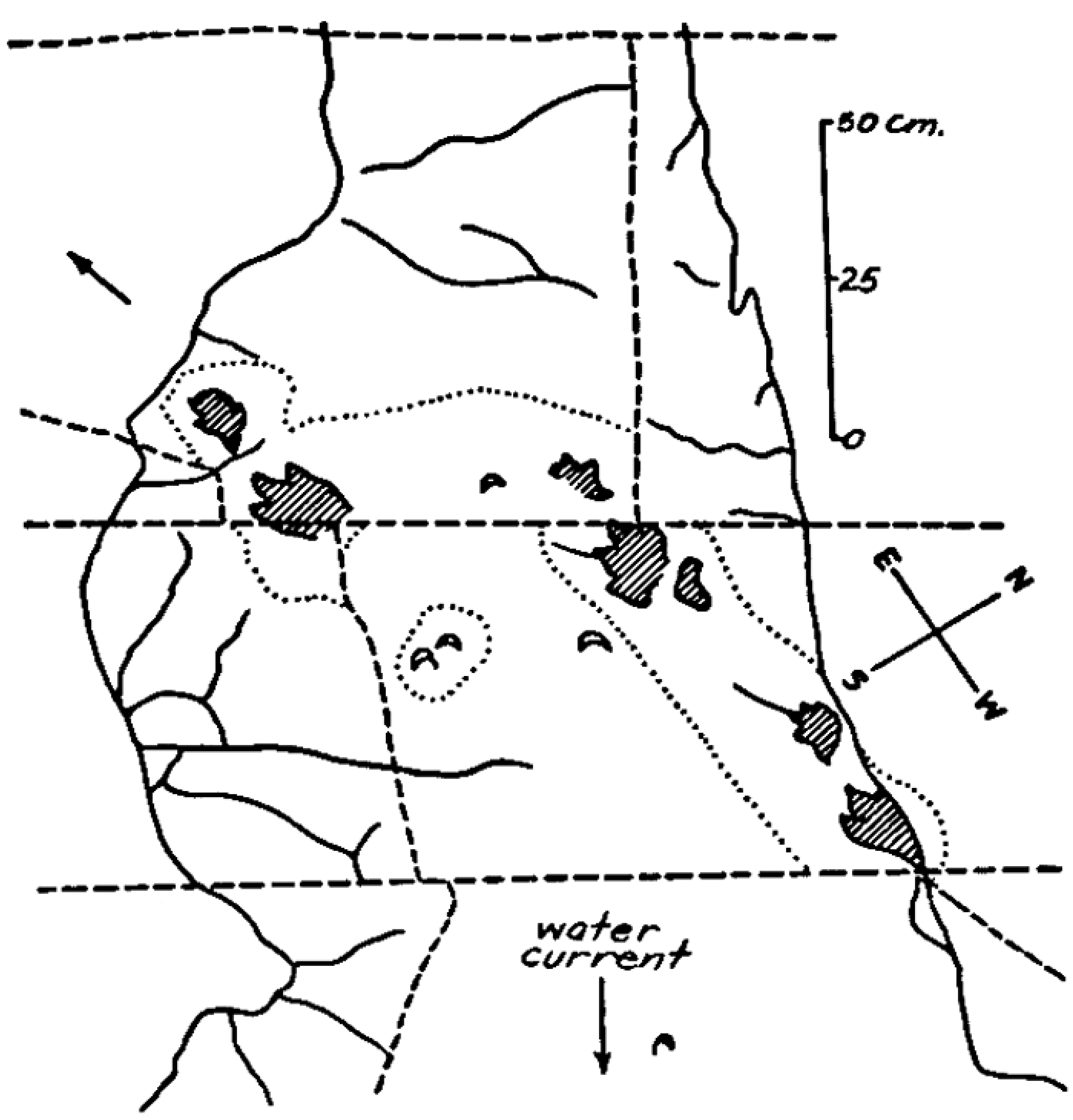

Fig. 29. Trackway surface from amphibian quarry near Meteor Crater, showing a large chirotheriid crossing a shallow stream channel. The reptile crossed the partly dry bed, going upstream (east) as indicated by crescentic ridges formed around clay pebbles. Original thin layer of marl was apparently sticky when the reptile crossed over but subsequently developed a definite pattern of cracks. (Dashed lines indicate individual slabs, dotted lines the part collected. Surface cast in limey sandstone.)

in having a peculiar "flat-footed" pes in which the individuality of pes digits I–IV is carried from the hypex over the metatarsal-phalangeal axis into the proximal border of the digit group. Also the proximal border bulges proximally instead of showing the broad indentation of other chirotheriids. Pes digit V, including its phalangeal part, is massive; the metatarsal pad is massive and elongated proximally to a tarsal heel.

These giant species cannot be compared at present with the giant *C. herculis* of Europe which also is apparently a large-manus chirotheriid. The giant species described here may be represented in Europe but the tendency has been to include all large chirotheriids in *C. barthi*, or in a *C. barthi* "group," whether they be of the large-manus or small-manus type. The set of footprints (pes over 30 cm.) designated by Soergel, fig. 39, as *C. barthi* is almost certainly not this species but a giant species resembling *C. moquiensis* and *C. rex*.

Chirotherium sp. indet.

A number of footprints collected from the Moenkopi are too imperfect for specific designation. Some of these are "running tracks" similar to those described by Soergel (1925). Most are indistinct because of the character of the recording surface. Several trackways had to be left in the field for reasons already stated. Certain of the collected and uncollected footprints furnish information necessary for full appreciation of the Moenkopi chirotheriids.

No. 37341, fig. 29

A series of 3 consecutive steps of a large species was discovered in the Lower Moenkopi at Meteor Crater. The trackway surface is a westward extension of that which contains the trackways of *C. diabloensis* and *C. minus* (fig. 21).

The animal walked across a narrow, shallow channel in which a thin layer of marl mud had been deposited. Apparently the mud was very slippery and sticky and adhered to the animal's feet, for the impressions lack critical detail. The individual width of the widespread digits of the pes is much wider than it ought to be. Presumably the action of the foot on the slippery surface was the cause.

The stride is 98 cm., the pace angulation 140 degrees, and the ratio of stride to pes length is 4.7 to 1. The overall dimensions of manus and pes are 10 cm. long by 9.5 wide and 21 long by 14.5 wide, respectively.

The relatively large size of the manus excludes this species from the small-manus group and the character of the pes excludes it from the contemporaneous *C. diabloensis*, *C. minus*, and the "flat-footed" giant chirotheriids. The impressions resemble *C. barthi* from the Upper Moenkopi in general outline, but the trackway, if accepted as typical, is notably wider, having a pace angulation of 140 degrees compared with 170 degrees. Probably a clearly impressed trackway would prove different from *C. barthi*.

SMALL-MANUS CHIROTHERIIDS FROM THE MOENKOPI

Chirotherium coltoni n. sp.

Type.—Univ. Calif. Mus. Pal. no. 37329, isolated set of manus and pes impressions, fig. 30, pl. 44.

Horizon and locality.—Lower Moenkopi near Meteor Crater, Arizona; U.C.M.P. loc. V3835, loc. map at "b."

Diagnosis.—Small-manus chirotheriid with pes digit IV noticeably shorter than II; pes length 12.2 cm.; pes digit group I–IV relatively long and metatarsal pad on pes digit V relatively unexpanded compared with those of other small-manus chirotheriids.

Discussion

This isolated set of manus and pes impressions represents a significant discovery. The footprints are those of a specialized chirotheriid with a reduced manus, yet the horizon at which they were found is several feet lower than that at which the most primitive chirotheriid, *C. diabloensis*, occurs. The new

Fig. 30. *A*, *Chirotherium coltoni* (type), isolated set of manus and pes impressions from Lower Moenkopi near Meteor Crater, drawn from specimen shown in pl. 44; *B*, *Chirotherium marshalli*, manus and pes based on composite detail of footprints shown in fig. 31, *A*.

species is named for Dr. H. S. Colton, Director of the Museum of Northern Arizona.

Measurements are included with those of *C. marshalli*, a related form, from the Upper Moenkopi.

No. 37329 (type)

The impressions are preserved in cast on the underside of a cross-bedded lens of sandstone. The orientation or extent of the trackway surface is not known. The pes is clearly and deeply impressed so that much of the metatarsal region is visible. The manus is less well impressed, particularly digit V.

The relatively small manus is 9 cm. in front of the pes and in line with pes digit I. The separation is wide but not of particular significance unless a full trackway should prove it to be the rule. The manus is turned out slightly more than the pes if the axis of III is the criterion.

Manus.—The manus is broad relative to its length, 4.2 cm. by 3.1 cm., owing in part to the incomplete impression of digit V. Its general size is smaller relative to the pes than any Moenkopi species except *C. marshalli*. Digits II–IV are short and wide with less free length than communal length. The tips of the digits give no indication of claws but II and IV come to a point within a broad angle. All the digits including V are bunched together in marked contrast with contemporaneous species.

The general pattern and relative size of the manus is like that of *C. marshalli* and can be better understood from a description of particularly clear impressions of this species.

Pes.—The pes is thick-toed, stout, and 12.2 cm. long by 8.3 wide, overall. The extreme shortness of digit IV is the most salient character.

Digit group I–IV is relatively short and broad compared with that of primitive species but is less so than related *C. marshalli* from the Upper Moenkopi. Digit III exceeds II by 1 cm., IV by 2 cm., and I by 3 cm. Digit I is slender in contrast with the thickness of digits II–IV. Thick digital pads on these digits obscure the position of phalangeal joints, certainly a contrast with the "naked" toes of nearly contemporaneous *C. minus*.

The metatarsal-phalangeal axis is thickly padded. A large, centrally located "high" in the contour of the impression suggests the communal pad of *C. barthi*. The proximal border of digit group I–IV is distinguished from the metatarsal region by a slight break in contour. The border is broadly indented between the base of I and IV. Taken together these characters suggest a well-defined, transverse arch in metatarsals I–IV, distally, but not as strong an arch as in *C. barthi*.

Heavy but narrow claws of triangular outline are indicated on digits II–IV. The ends were blunted presumably from wear. A probably similar claw on digit I distorted its impression. No claw is indicated on digit V even though its tip is deeply impressed.

Digit V has an expanded base comparable to *C. barthi*. While it is much more strongly developed than in contemporaneous *C. minus*, it lacks the massiveness seen in related *C. marshalli* from the Upper Moenkopi. The phalangeal part of digit V is relatively robust but the recognized tendency of this part of

digit V toward enlargement due to extramorphologic agencies tempers its significance. There is no furrow or break in the contour of the surface plane to set off the phalangeal part as in *C. marshalli* and other species in which the functional importance of the phalangeal part is reduced.

The metatarsal region is deeply impressed but there are no ridges indicating the position of the metatarsals as noted in *C. diabloensis, cameronensis, minus,* and *barthi.*

Relationships

The combined characters of *C. coltoni* definitely separate it from other Moenkopi chirotheriids except *C. marshalli,* which it resembles in having a small manus and very short pes digit IV. It differs from this form by having a relatively longer pes digit group I–IV; pes digit III is relatively longer; the basal pad of digit V is less massive, the phalangeal part being more sturdy; the manus is slightly larger relative to the pes.

The special significance of *C. coltoni* lies not so much in its possible ancestral relation to *C. marshalli* as in the fact that it proves that specialized, small-manus chirotheriids appeared early in the Lower Triassic, and were not developed later, as Soergel has suggested, from species such as *C. barthi.*

Chirotherium marshalli n. sp.

Type.—Univ. Calif. Mus. Pal. no. 37348, trackway of 2 consecutive steps, fig. 31, pl. 44.

Referred specimens.—U.C.M.P. nos. 37349–50, isolated footprints from same trackway surface and of about same size as type.

Horizon and locality.—Upper Moenkopi near Penzance, 5 miles west of Holbrook, Arizona; U.C.M.P. loc. V3956, Penzance loc. map at "B."

Diagnosis.—Small-manus chirotheriid with pes digit IV noticeably shorter than II; pes length 22 cm.; pes digit group I–IV as broad as long, pes digit V with large ovoid metatarsal pad and reduced phalangeal portion; trackway apparently very narrow, pace angulation near 180 degrees, and ratio of stride to pes length 5 to 1.

Discussion

The short trackway of two consecutive steps and the two isolated sets of manus and pes impressions upon which the new species is based represent the same or very similar individuals. The species is named for my friend and field companion in 1939, Mr. Joe T. Marshall, Jr., of the Museum of Vertebrate Zoölogy, University of California.

The footprints occur on the underside of a sandstone ledge outcropping on the north side of a butte 5 miles west of Holbrook. The level is 130 feet above the base of the Moenkopi and well above the middle gypsum zone. The trackways run at right angles to the outcrop so a consecutive series of steps is very difficult to obtain except by large-scale excavation. The footprints were originally made in sand, not the usual mud, and the sandstone which cast the impressions is coarse and friable. As a result the footprints are not so clear or resistant to weathering as other Moenkopi trackways. Obscure footprints of small indeterminate species of *Chirotherium* and of *Rotodactylus* occur on the same surface.

Measurements of *C. marshalli* are included in table no. 13 with those of related *C. coltoni* from the Lower Moenkopi.

No. 37348 (type) fig. 30, *B*

The four footprints of the two consecutive steps are nearly in line with each other, indicating a very narrow trackway pattern and therefore a high pace angulation of 170–180 degrees. The pace is 51 cm. (stride, 102 cm.) and the

TABLE 13

COMPARATIVE MEASUREMENTS OF *Chirotherium colloni* AND *C. marshalli*
(in centimeters)

Measurements	*C. colloni*, No. 37329	*C. marshalli*		
		No. 37348	No. 37349	No. 37350
Pace angulation (in degrees)	....	(180)[a]	....	....
Stride	....	(102)	....	....
Pace	....	51	....	....
Manus:				
Over-all L	3.2+	6.5	Obscure	7.0
W	4.8	....		7.0
Digit I–IV L	2.5	....		4.7
W	3.7	....		5.7
Digit III L	2.4	4.0		4.0 (1.8 free lgth.)
At hypex W	....	....		2.0
Pes attitude to midline (degrees)	....	15	....	
Pes:				
Over-all L	12.2	22.5	22.0	Only tips of digits preserved
W	8.3	13.5	13.0	
I–IV L	7.8	11.5	12.0	
Max. W	6.7	12.0	12.0	
At base W	5.3	9.5	9.5	
I–IV divarication (in degrees)	30	40	40	
Digit length:				
I	4.6	8.0	8.0	
II	6.7	10.0	....	
III	7.6	11.0	11.0	
IV	5.8	8.5	8.5	
V	5.9	11.0	11.0	
Phalangeal part of V	....	3.0	3.0	

[a] Figures in parentheses are estimated.

relation of stride to pes length is 5 to 1. The axes of left and right pes digit III make an angle of 30 degrees, therefore each pes is turned out 15 degrees from the midline.

The small manus occurs just in front of the pes and is oriented similarly. It is obscure in step 1 and partly distorted in step 2. Full detail is provided by an isolated impression no. 37350. The pes is obscure in step 1, except for digit V, and clearly impressed in step 2. But here the phalangeal part of digit V is ob-

scured by another footprint. Full detail of digit V is provided by step 1 and by isolated pes no. 37349.

Manus.—The overall dimensions are relatively small compared with the pes, 7 by 7 cm. and 22 by 13 cm., respectively. In general character the manus is chirotheriid-like, but it differs from all other species except *C. coltoni* in having short, sturdy digits bunched tightly together. Digit V is closely appressed to digit group I–IV and appears to have functioned with it as a unit.

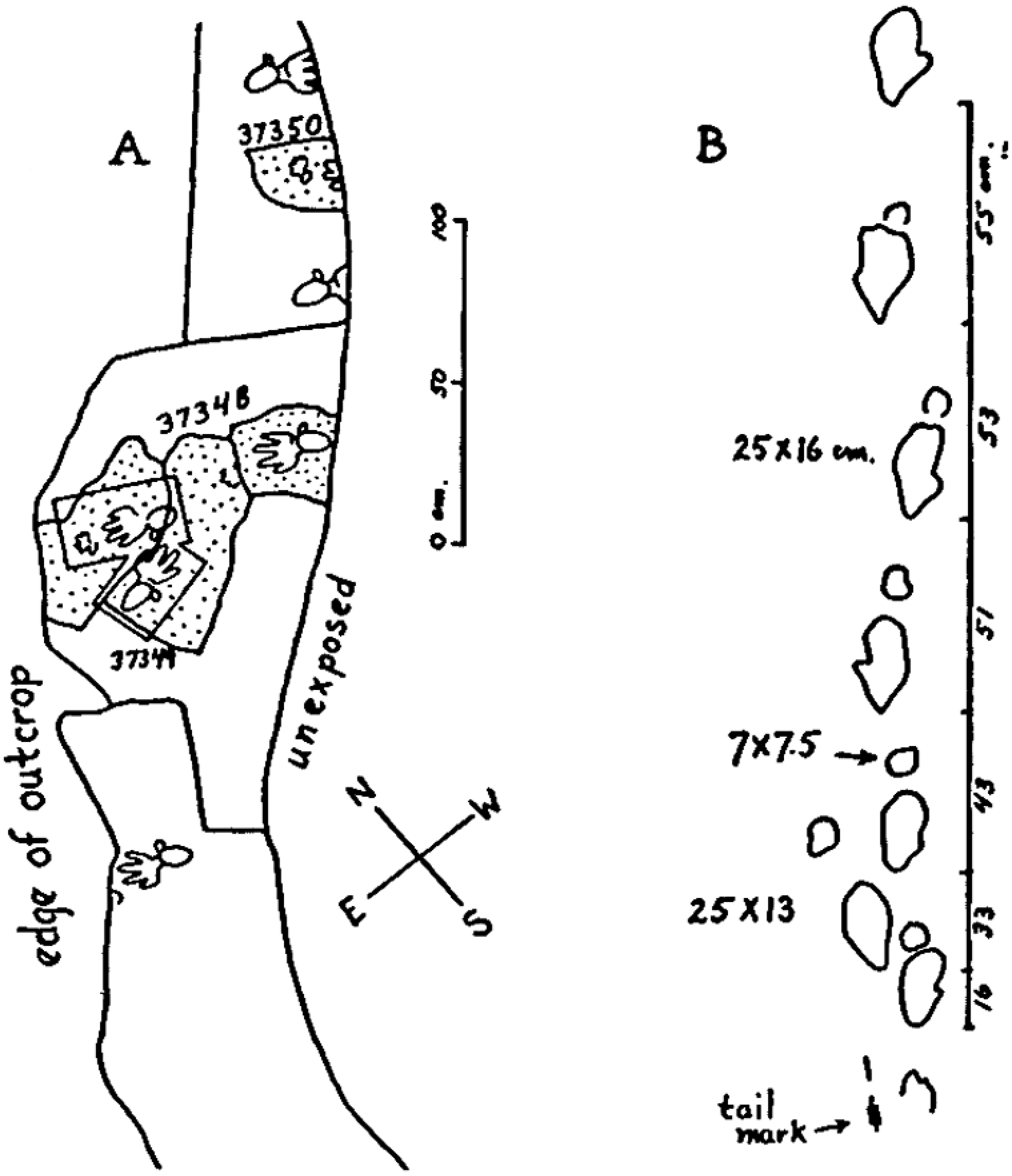

Fig. 31. *A, Chirotherium marshalli;* diagram of a series of slabs containing footprints (cast); stippled area collected; rectangles enclose areas shown in pl. 44. *B, Chirotherium* cf. *marshalli;* arrested trackway, showing acceleration of pace from standing start; note that manus accompanies the pes even in the arrested position; trackway not collected; sketch from author's notes, 1939, p. 141.

The digits have a very short free length and are broadly pointed. The pad on each digit is devoid of transverse furrows or other signs of differentiation. There is no indication of claws but, as in *C. barthi,* the claw may have been engulfed or at least underlain by a thick digital pad.

Pes.—The pes is distinguished mainly by relatively short digits I–IV and by a large ovoid metatarsal pad on V. Digit group I–IV is as wide as it is long and digit IV is markedly reduced in length, thereby contrasting strongly with long-toed primitive species. Digit III exceeds II by 1 cm., IV by 2.5 cm., and I by 3 cm. Undifferentiated pads cover the free length of the digits. The base of II and III is lost in a large central "high" suggestive of the communal metatarsal-phalangeal pad of *C. barthi.* The posterior border of digit group I–IV is broadly indented between the base of I and IV. Digits I–IV diverge a total of 40 degrees.

Heavy, blunted claws on digits II–IV appear to be intermediate between the triangular claw of *C. barthi* and the spatulate claw of *C. rex*. The claws seem to have been exceptionally heavy for the size of the digit. The impressions are undistorted and no other interpretation is possible. The claw on digit I is narrower than the others.

The phalangeal part of digit V seems reduced to a nearly useless role as it protrudes from the massive ovoid pad something like the stem of a squash. It is set off from the pad by a shallow furrow and a general break in the contour of the impression. The ovoid metatarsal pad is relatively larger than in other chirotheriids except *C. rex* and *C. moquiensis*, where it is more elongate and angular in outline. It apparently extended proximally to a tarsal heel, indicating a relatively prone position of the metatarsal bundle. There is no doubt that the expansion of the pad is real and characteristic of the impression in contrast with the occasional expansion seen in species with a smaller pad, for example, *C. barthi*.

The metatarsal region is well impressed but metatarsal ridges are not evident. The metatarsal region between the base of digit V and digit group I–IV appears to have been an important weight carrier in *C. marshalli*.

Chirotherium cf. *marshalli*

A most interesting trackway of a small-manus chirotheriid was found on the underside of a massive ledge a short distance west of the ledge which carried the type of *C. marshalli* and at approximately the same level (Penzance loc. map at "A"). The trackway was not collected but measurements and drawings were made (fig. 31, *B*).

The long trackway runs parallel to the outcrop. It was deeply but poorly impressed in the original sandy surface and is poorly preserved by cast in a coarse and friable blue sandstone. The individual footprints are chirotheriid in general outline and resemble *C. marshalli* in size and particularly in their reduced manus. The trackway pattern shows where a chirotheriid paused and then proceeded from a standing start with a progressive increase of pace from 16 to 55 cm. A short, keeled impression of the tail is associated with the first visible footprint. From its position it cannot indicate a sitting posture associated with arrested locomotion but rather an accidental contact with the ground as the animal accelerated from its arrested position. The most interesting fact is that the trackway is fully quadrupedal, even though the animal apparently came to a full stop. It is believed that this evidence proves what is indicated by the majority of trackways, namely that chirotheriids were habitually quadrupedal.

Relationships

The special significance of *C. marshalli* lies in the following facts. The narrow trackway is fully quadrupedal despite the reduced manus. The small manus is hooflike and was probably useless as a grasping organ. Pes digit V is specialized to carry nearly half of the weight borne by the pes, yet the pes is not so "flat-footed" as in *C. rex* or *moquiensis*.

One cannot overlook the fact that the reduced manus is a relatively simple

indication of a complex set of skeletal differences. An important backward shift of the center of gravity is indicated. It follows that many differences existed between the skeleton of a typical chirotheriid, *C. barthi*, and that of a small-manus species. In the footprints themselves, characters such as the marked reduction of pes digit IV seem to be associated with a relatively small manus. For these reasons the Chirotheriidae is believed to be divided into a large-manus and a small-manus group. Nevertheless, the evidence shows that both groups were fully quadrupedal and at least in larger forms the manus was hooflike and probably incapable of a grasping function.

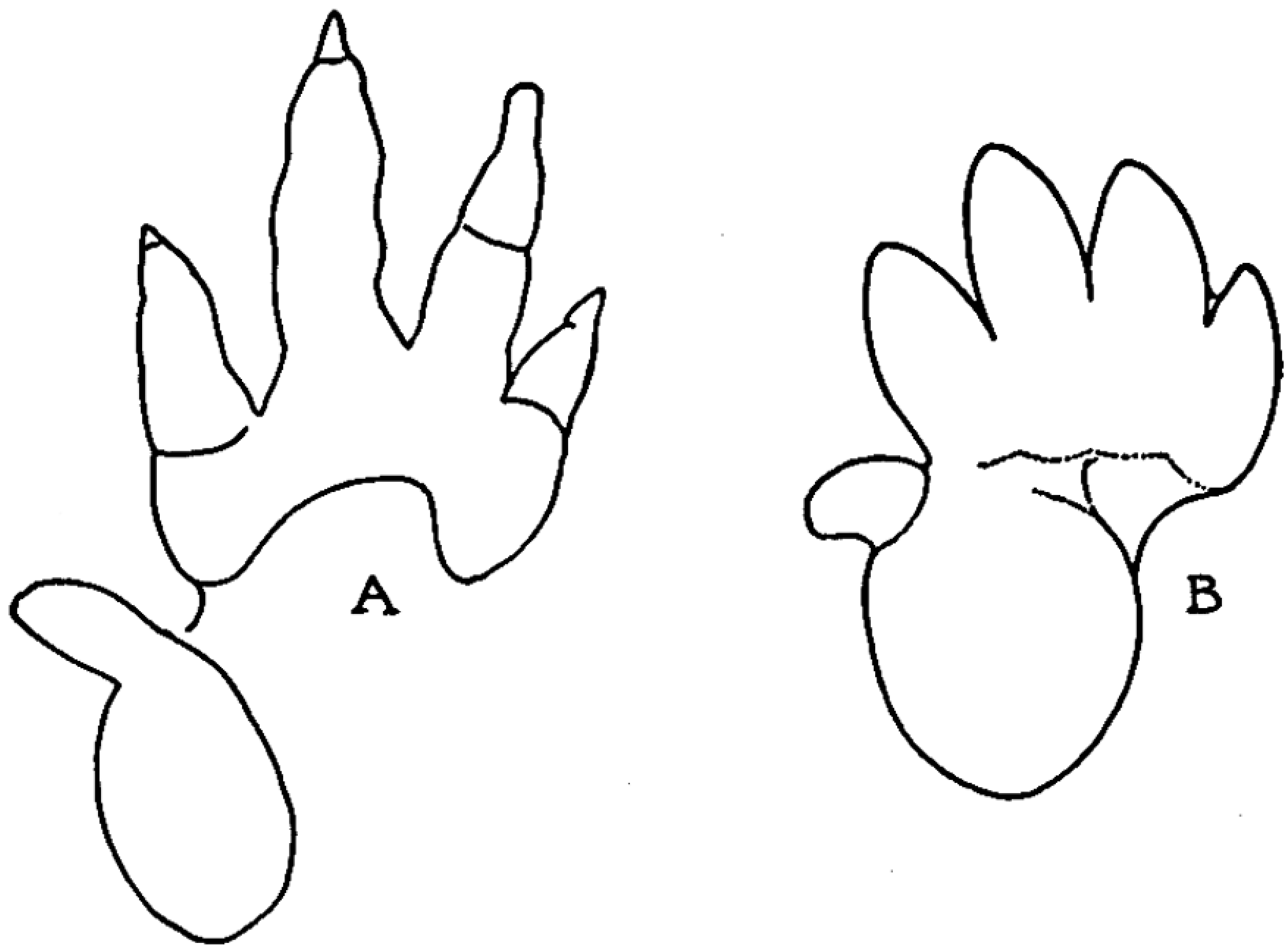

Fig. 32. *A*, pes representing Beasley's group A4, named here *Chirotherium beasleyi* n. sp.; drawing enlarged from Lomas, 1907; *B*, giant pes of small manus chirotheriid included in *Chirotherium barthi* "group" by Soergel; drawing after photograph by Soergel, 1925, fig. 31.

C. marshalli is clearly related to *C. coltoni* more closely than to other Moenkopi species, particularly in the reduced manus and reduced pes digit IV. Important differences are: relatively longer pes digits I–IV, unexpanded metatarsal pad of digit V, and narrower claws in the earlier form. These differences are what one would expect if the latter form had developed from the earlier one. The evolution of *C. marshalli* from *C. coltoni* is a unique possibility at present since the better represented species of large-manus chirotheriids fail to show anything of the sort.

A hitherto unnamed small-manus chirotheriid is known by excellent trackways from the English Keuper of Storeton (named *C. beasleyi* here; see discussion on p. 345). The well-known figure that was published by Lomas (1907) shows five consecutive steps of a narrow trackway with a low ratio of stride to pes length, 4.2 to 1, and with the pes well turned out from the midline. The extremely short pes digit IV and relatively small manus particularly suggest relationship with *C. marshalli*. The English species differs from both Moenkopi species in having generally slender digits for such a large animal, and pes digits I–IV with knobby outline apparently lacking thick, undifferentiated digital pads (fig. 32, *A*). Pes claws were apparently sharply triangular in outline.

Pes digit V resembles *C. marshalli* except for lesser expansion of the median border of the pad; this is often variable with depth of impression.

The giant pes 33 cm. long assigned to the *C. barthi* "group" by Soergel is similar to *C. marshalli* except for size (fig. 32, *B*). As indicated earlier, similar pes impressions known to be associated with relatively small manus impressions are referred to *C. barthi* var. *herculis* by Lilienstern (1939).

A Possible Bipedal Chirotheriid

The existence of a bipedal species of chirotheriid is indicated by an uncollected specimen found in the Lower Moenkopi of Moqui Wash (Moqui Wash loc.

Fig. 33. Species of *Chirotherium* from the Moenkopi formation assembled to show relative size. Left to right, *C. rex, C. moquiensis, C. barthi, C. minus, C. cameronensis* (upper), *C. diabloensis* (lower), *C. coltoni, C. marshalli.*

map, NE. corner of section 25 at "x"). The level is approximately the same as that of the type of *C. moquiensis* found 1 mile to the north.

While excavating a hole for a telegraph pole, workmen had quarried out a huge slab of thick sandstone. They left it bottom side up near the excavation. I was able to obtain a photograph (pl. 45) by standing on the top of our field car. The slab was still there and undamaged in July, 1946.

The undersurface of the slab shows many lacertoid reptile tracks, among which are two consecutive pes impressions of a large chirotheriid. The interpretation of the trackway depends largely on the importance attached to the apparent absence of manus impressions.

The pace is 63 cm., hence the stride would be approximately 125 cm., and the ratio of stride to pes length is 5 to 1. The pes is about 24 cm. long. Orientation of the footprints indicates a narrow trackway with the midline running through digit II. In a typical chirotheriid trackway the manus should occur just in front of the first pes impression and another ought to occur behind it within the included surface of the slab. Not even a faint toe-tip impression can be seen in the expected positions. The lack of a manus cannot be attributed to a running gait because the evidence of the footprints points to a slow walk.

This chirotheriid trackway is the only one discovered in the Moenkopi which seems to indicate a bipedal gait. The pes itself cannot be readily identified with any other species. Digit V and the indented posterior border resemble some footprints of *C. barthi*, but digit group I–IV is proportioned more like the broad pes of *C. rex*. In any event the erection of a new species must await the collection of material which is complete enough to show the habitual use of a bipedal gait. Until then the existence of a truly bipedal chirotheriid in Moenkopi time rests on the meager evidence presented here. Meager though it may be, this evidence is based on a trackway of undoubted chirotheriid affinities. This cannot be said of the Keuper trackway described as *Chirotherium bipedale* (Abel, 1935).

Classification of the Species of *Chirotherium*

Much has been written of the characters of chirotheriid trackways and much has been inferred about the body characters of the animal responsible. It is generally apparent now that the trackways of *Chirotherium* represent a distinct family of early Triassic reptiles whose affinities lie well within the boundaries of the Pseudosuchia without conforming exactly to any known family (Soergel, 1925). The general similarity of the pes impression to a reversed human hand is characteristic.

Existing diagnoses of the family Chirotheriidae (Abel, 1935) and the genus *Chirotherium* (Soergel, 1925) are alike in containing characters pertaining to several different taxonomic categories and containing many inferred characters which are sound but somewhat impractical to use. There remains a need for a systematic treatment of chirotheriid trackways with the characters relegated as far as possible to their proper taxonomic category. Full utilization of trackway characters with a minimum of reliance on inferred characters seems most practical.

Studies of trackways and feet of living animals (Peabody, 1940; Taylor, 1944) show that the tetrapod trackway generally lacks specific characters but is usually diagnostic for the genus. It follows that most, if not all the characters used to differentiate species of chirotheriid trackways are actually generic when considered in relation to a taxonomic treatment of the living animal or of its skeleton. Many characters commonly used as generic are not less than ordinal, for example, pentadactyly. For these reasons it is felt that the chirotheriid species described here actually represent different genera. However, a practical treatment of fossil trackways requires the conventional use of the binominal system of nomenclature.

Presented below is a diagnosis of chirotheriid trackways from class to subfamily, together with a list of generic characters. The latter are commonly employed for specific identification of fossil trackways in the absence of truly specific characters.

CLASS REPTILIA

1. Maximum size (pes over 30 cm. long) 2. Plantar skin surface with granular or polygonal scales 3. Strong claws	eliminates Amphibia.
4. Phalangeal formula 2-3-4-5-3(4)	eliminates Aves, Mammalia

ORDER PSEUDOSUCHIA

1. Narrow quadrupedal trackway	eliminates all aquatic and flying reptiles and all land forms with sprawling gait.
2. Narrow quadrupedal trackway combined with pentadactyl, fully digitigrade feet	eliminates archosaurs excepting thecodonts.

FAMILY CHIROTHERIIDAE

1. Very small manus, large pes resembling reversed human manus. 2. Divergent, robust 5th digit, well developed as a crude, forward-directed prop. 3. Inferred dinosaur-like form with long slender fore limb.	eliminates Pseudosuchia of crocodile-like body form, and advanced, dinosaur-like Pseudosuchia, such as *Saltoposuchus*, which have a reduced pes digit V.

SUBFAMILY CHARACTERISTICS

Analysis of the chirotheriids from the Moenkopi and of the well-known species from Europe suggests a natural division of the Chirotheriidae into a large-manus group and a small-manus group, differing significantly from each other in inferred body proportions and hence in inferred skeletal characteristics, for example, in the pelvis. Each group contains primitive, advanced, and giant forms.

GENERIC CHARACTERISTICS

1. Size.
2. Variation in trackway pattern, for example, attitude of feet to midline, stride–pes length ratio, pace angulation.
3. Relative length of digits and metatarsals.
4. Attitude of the line of metatarsal-phalangeal joints I–IV to long axis of the foot.
5. Indicated length of metatarsals I–IV.
6. Relative proportion of digit group I–IV to rest of impression; also its length relative to its width.
7. Presence or absence of proximal separation of pes digits.
8. Relative proportions of pes digit V and of its phalangeal portion.
9. Development of specialized digital pads; character of plantar scales.
10. Absence of metatarsal-phalangeal pad on pes digit V, or if present, its shape and size.
11. Extent of functional surface of metatarsal V.
12. Size and shape of claws.

CLASSIFICATION OF SPECIES WITHIN THE FAMILY CHIROTHERIIDAE

1. Large-manus group.
   a) Small primitive species with slender digits, generally lacking specialized digital pads, relatively long pes digit IV:

C. diabloensis n. sp.	Lower Moenkopi
C. cameronensis n. sp.	Upper Moenkopi
C. hessei Soergel	Bunter of Germany
C. minus Sickler	Lower Moenkopi Upper Bunter of Germany

   b) Advanced species of large size with moderate development of specialized digital pads; pad of pes digit V large but localized around the metatarsal-phalangeal joint:

C. barthi Kaup	Upper Moenkopi Upper Bunter of Germany

   c) Giant species with massive foot structure, pes digit V being massive and possessing an elongate pad coextensive with the metatarsal; pes digit IV slightly shorter than II:

C. moquiensis n. sp.	Lower Moenkopi of Arizona; upper Moenkopi beds of Utah
C. rex n. sp.	Lower (?) and Upper Moenkopi
C. herculis Egerton	Keuper of England

2. Small-manus group; pes digit IV much reduced.
   a) Small species relatively primitive with relatively unexpanded pad on pes digit V; pes digit group I–IV relatively long compared to advanced species:

C. coltoni n. sp.	Lower Moenkopi

   b) Advanced species of large size with relatively short and broad pes digit group I–IV, large ovoid pad on pes digit V, which has weakly developed phalangeal portion:

C. marshalli n. sp.	Upper Moenkopi
C. beasleyi n. sp.	Keuper of England

   c) Giant species resembling *C. marshalli* but with pes more massively constructed and 33 cm. long:

"*C. barthi* group" Soergel (1925, fig. 31)	Bunter of Germany

3. A third category might include bipedal forms but the evidence for them is not conconclusive. It is certain that most of the chirotheriids were habitaully quadrupedal.

STRUCTURE OF *Chirotherium*

The physical character of the reptile, *Chirotherium*, has been reconstructed in a generally satisfactory manner by Soergel. He calculated the probable body form from proportions of the trackway pattern and reconstructed the pedal skeleton. His results apply mainly to the best known and original species, *C. barthi*. Discovery of American trackways of *Chirotherium* now makes it possible to interpret certain details more fully and sometimes differently. The following discussion will be concerned principally with the footprints and their bearing on the pedal anatomy of various chirotheriid species.

SKIN

At least some portion of clear impressions of the chirotheriid foot often shows a granular surface which represents the original scaled surface of the skin. Sometimes an exceptional specimen will show such detail over much of the plantar surface. The scales tend to be granular, and when they are close to-

gether the individual scale presents a polygonal, often hexagonal outline. Pseudo skin impressions also occur but these can be detected by careful observation. For example, the mudflat surface itself may have a granular texture which extends over the footprints as well as surrounding areas. One series of *Chirotherium barthi* footprints in the Museum of Northern Arizona (no. G2.2612) shows a very coarse, polygonal pattern but this seems to have originated when seepage water in the fresh footprints evaporated and the fine mud in the depressions cracked into a polygonal pattern.

The size of scales on the plantar surface is small even in large *C. barthi*. The minimum diameter is about 1 mm. in *C. diabloensis* and the maximum is 5 mm. in a giant form from Utah (pl. 41). Some indication of a scaly surface is definite in all the Moenkopi species except *C. rex* and *C. marshalli*. Better material for these species will undoubtedly show a scaly plantar surface. Certain European specimens of *C. barthi* and *C. hessei* show the skin surface clearly (Soergel, figs. 11, 12).

The plantar scales seem to be of a size on all areas of the foot in most species. However, in the Utah form there is a definite size range on the pes of from 2 to 5 mm. in diameter. The largest scales occur on the median metatarsal region, on the pad of digit V, and on the metatarsal-phalangeal pad at the base of digit III. The smallest scales occur along the lateral border of the distal half of digit IV. In addition, the largest scales tend to be flattened instead of rounded or beadlike. Unfortunately, the distal portions of all the digits were defaced by weathering; nevertheless, this specimen is unsurpassed for detailed impression of the skin surface.

Soergel has noted that the granular scales along the plantar border of the digits caused vertical furrows on the edges of deep digit impressions. Although this is true, American specimens clearly indicate that fringe scales comparable to those of recent lizards were responsible for some of the vertical furrows. On a large footprint of *C. barthi* in which the plantar scales do not exceed 3 mm. in diameter, the regular spacing of deep furrows on the lateral border of pes digit III indicates a fringe-scale width of 6 mm. On the giant pes from Utah the fringe scales along the lateral border of digit V were 8 mm. wide; along the lateral margins of digits III and IV they were 6–7 mm. wide. The free border of the individual fringe scale was generally convex but so ragged that many close-spaced scratches were superimposed on the larger convexity.

The usual presence of vertical furrows on the *lateral* border of deep impressions are an expression of the gait of *Chirotherium* and do not preclude the presence of fringe scales on the median border of the digits. Well-developed fringe scales on the chirotheriid foot may have helped somewhat to support the weight on a soft surface. However, most footprints show only the plantar surface with its granular scales.

SPECIALIZED DERMAL PADS

It has not been fully appreciated that the development of dermal pads in chirotheriids varies considerably. In some forms the dermal covering of the sole is approximately unpadded as in recent lizards. Here the position of a

skeletal joint may be indicated by a bulbous enlargement. Mesarthral areas are broadly constricted. And some chirotheriids have extensive, specialized pads which may cover the whole digit, effectively concealing any indication of the pedal skeleton. A similar condition may be seen in the ratite bird, rhea.

Certain forms, including the typical species *C. barthi*, are intermediate in the development of dermal pads. Transverse linear furrows in the digital pads sometimes indicate mesarthral constrictions and sometimes do not. They rarely if ever coincide with a skeletal joint. This fact has been generally overlooked in literature dealing with trackways. The manus of chirotheriids is more likely to show undifferentiated digital pads than the pes.

The dermal covering of the metatarsal-phalangeal axis may or may not show divisions corresponding to the metatarsal-phalangeal joints, I–IV. Sometimes the posterior or proximal border of digit group I–IV indicates a fourfold division. Less often the indication is carried across the axis by linear furrows as in the giant species *C. rex* and *moquiensis*. In the typical species, *C. barthi*, a threefold division occurs in which a large central pad covers the base of pes digits II–III. This is interpreted here as indication of a high transverse arch formed by metatarsals I–IV.

The dermal covering of pes digit V is of particular interest. Primitively it seems to have been merely thickened without any apparent differentiation. The first indication of a small specialized pad appears at the position of the metatarsal-phalangeal joint in *C. minus*. In *C. barthi* the pad is large and round but still centered around the metatarsal-phalangeal joint. In the giant species of large-manus chirotheriids the pad is long and massive and extends posteriorly to the proximal end of the metatarsal. In the small-manus chirotheriids the pad is also large but ellipsoid in outline and apparently extends backward to the proximal end of the metatarsal.

CLAWS

The presence of strong claws on the first 4 digits of chirotheriids is well established. Their character has not been well understood except in *C. barthi*. It is now evident that the shape of the claws differs widely. In the small forms the claw was generally long and laterally compressed with a sharply pointed or blunted end. In the typical species it was massive, blunted, and broadly triangular in outline. In certain species, particularly *C. rex*, the claw was massive and scoop-shaped with a spatulate outline. Such a hooflike claw suggests that the Chirotheriidae included herbivorous as well as carnivorous species. In all species the claw was rooted well back in the body of the digit, commensurate with its powerful development.

Much importance has been given to the presence or absence of a claw on digit V. The American and European material shows only that digit V of chirotheriids possessed a vestigial claw or none at all. Often the tip of the divergent digit is so distorted as to show a spur which might be incorrectly interpreted as a claw mark. If a strong claw were present, it could be reasonably expected to leave a trace in consecutive impressions. There is the distinct possibility that the claw was either so high in position or so engulfed by a thick, calloused skin that we have no consistent record of its presence.

The "great toe" (V) of chirotheriids may be compared with that of the primate, orang-utan, in which the "great toe" (I) is carried at nearly a right angle to the long axis and the terminal phalanx may be absent, fused, or vestigial and may lack the nail (Hooton, 1942, p. 120). In any event the claw on the fifth digit of chirotheriids is not of much use as a specific character unless it is clearly indicated in consecutive steps of a trackway. Such a trackway has not been observed.

Manus digit V of the giant American species, *C. rex*, seems to have had a heavy claw of broad triangular outline in contrast to the spatulate claws on pes I–IV. This is the best evidence of a claw on digit V provided by American material.

It is often difficult to distinguish claw marks in isolated footprints because the digit tip is so liable to distortion by movement of the foot. A number of consecutive and clear impressions usually are necessary for valid conclusions. This is particularly true of the manus, where thickened digital pads seem to underlie much of the claw. In large chirotheriids it is difficult to tell whether the broadly pointed or rounded tip of the digit represents the claw or whether the digital pad is continuous to the tip. In general the manus claw of large forms appears to have been stubby, robust, and partly engulfed by a massive digital pad.

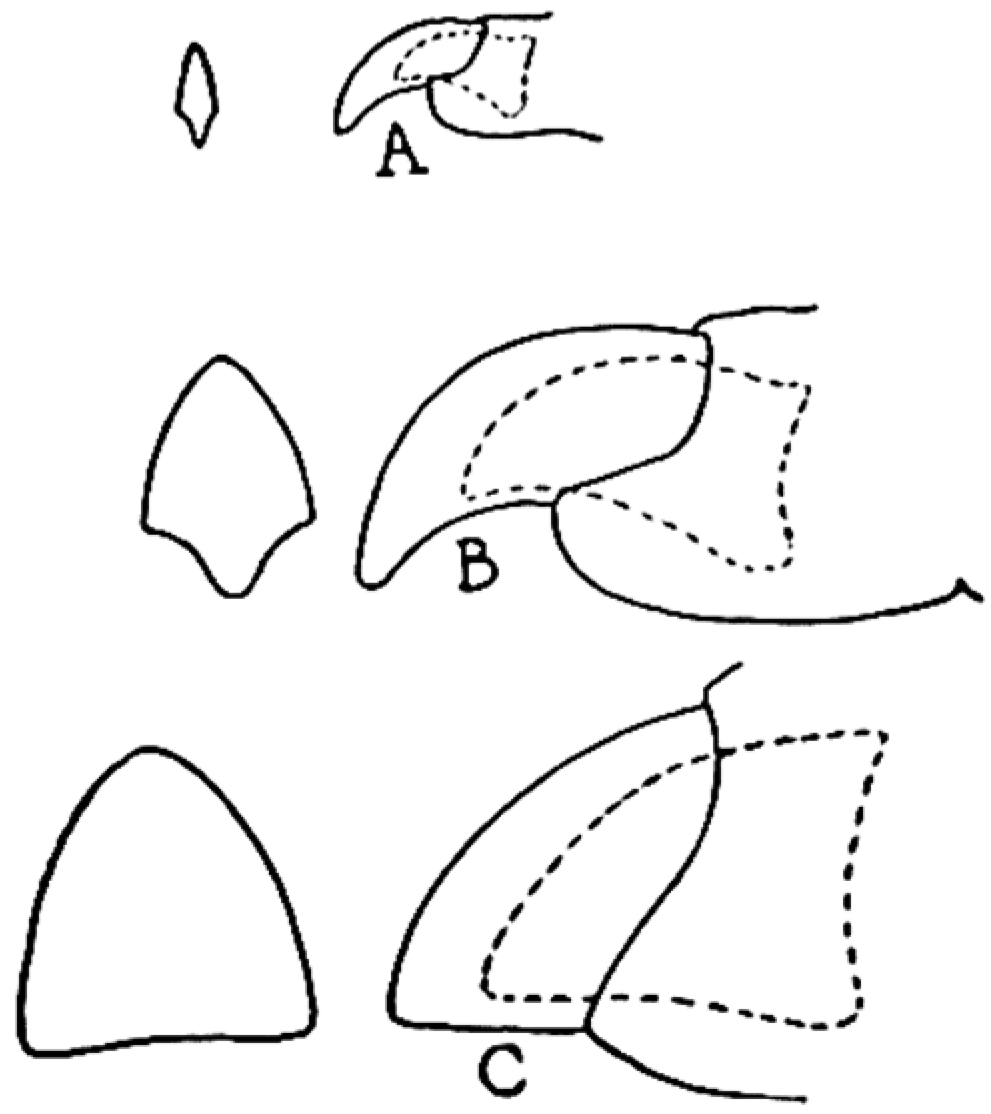

Fig. 34. Reconstruction of claw outline of digit III: *A, Chirotherium minus; B, C. barthi; C, C. rex.*

PHALANGEAL FORMULA

In order to interpret properly the pedal skeleton of chirotheriids the feet of a number of living animals were examined; sphenodon and iguana among reptiles, and particularly the tinamous, apteryx, rhea, pigeon, and domestic turkey among birds. In the unpadded foot of reptiles the position of a phalangeal joint is likely to be indicated by a bulge, the mesarthral region by a constriction. The plane of the joint bisects the bulge transversely, except in the terminal bulge. Here, the terminal joint involving the claw phalanx tends to occupy a position proximal to the center of the terminal bulge.

The avian foot is padded in various ways, two of which concern us here. The most common is the development, below the joint, of a pad which carries most of the weight. The pad is bounded proximally and distally by a transverse flexure crease in the skin. There may be two mesarthral creases per segment in digit III, one in digit IV. It is clear that the pads underlie the joint; a transverse crease never coincides with a joint except terminally. Here the pad underlying the claw tends to be distal to the terminal joint. The footprint of a domestic turkey will best illustrate the relation of the pedal skeleton to the contours of the impression (fig. 37, *C*).

In the foot of the rhea, extensive pads are developed which effectively conceal the position of the phalanges. Such transverse creases as occur do not coincide with the position of any joint (fig. 35, *A*).

Application of the foregoing observations to certain fossil footprints leads to conclusions differing from those of Lull and Soergel. The reconstructed pedal skeleton of a three-toed dinosaur, *Grallator cursorius* Lull, takes on somewhat different and more natural proportions (fig. 37, *A*, *B*). Of more immediate concern, the pedal skeleton of a large chirotheriid reconstructed by Soergel has quite different proportions if reconstructed in accordance with the foregoing observations (fig. 38, *A*, *B*). The differences in the two reconstructions arise wholly from differences in the interpreted position of phalangeal joints. The interpretation given here is believed more nearly correct because

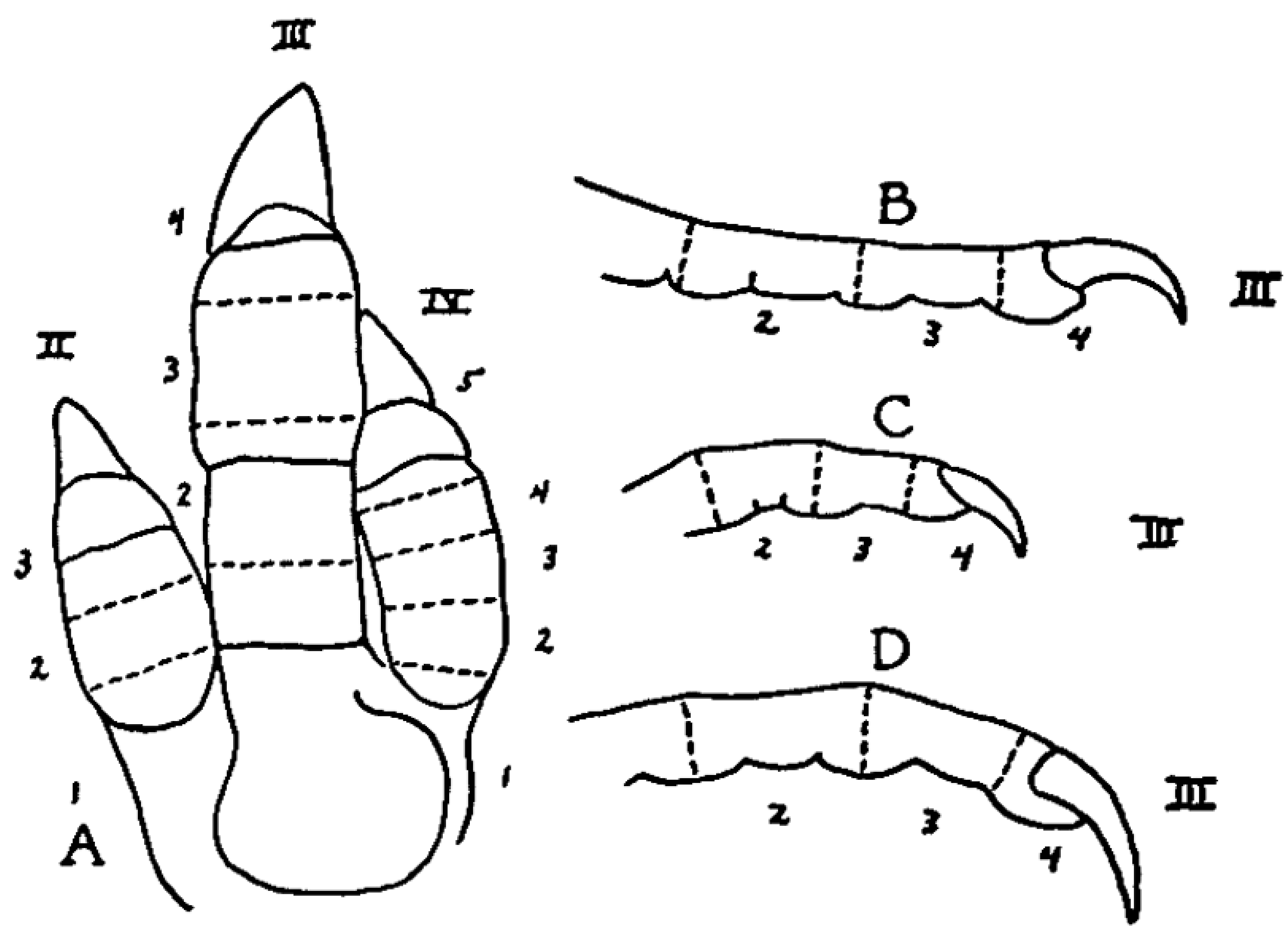

Fig. 35. *A*, position of phalangeal joints in foot of the rhea (Univ. Calif. Mus. Vert. Zoöl. no. 42731); *B*, *C*, and *D*, position of phalangeal joints in digit III of pigeon, tinamous, and apteryx, respectively.

it agrees with data from living animals and also agrees with the clear picture of the pedal skeleton given by unpadded footprints of certain small chirotheriids.

The reptilian phalangeal formula, manus 2–3–4–4(5)–2(?), pes 2–3–4–5–2(3), has been determined for *Chirotherium* by Soergel on the basis of his generalization that the largest number of phalanges belong to the longest toes, the smallest number to the shortest toes, and on what is believed here to be an unsatisfactory interpretation of the position of phalangeal joints in *Chirotherium barthi*.

As indicated earlier, *C. barthi* is intermediate in the development of specialized digital pads, and the position of phalangeal segments in the manus digits and in pes digits III–V is not indicated in the footprints. We must turn to the unpadded feet of the small species *C. diabloensis* and particularly *C. minus* to find the most positive indication of the phalangeal formula. There can be little doubt that the bulges in the digit impressions of these species represent the position of skeletal joints. On this basis clear impressions of the pes indicate 2 phalanges in pes I, 3 in II, 4 in III, and 5 in IV. The anatomy of pes digit V is nowhere better shown than in American examples of *C. minus*. The slight expansion at the base of digit V can only indicate the position of the

metatarsal-phalangeal joint. With this as a reference point the angular outline of the distal medial border of V indicates no less than 3 phalanges with a probably aborted fourth phalanx.

There is little in any chirotheriid manus to indicate the phalangeal formula except for its general similarity of proportion to the pes. In clear impressions of small *C. diabloensis* (pl. 35, *C*), a partial formula, 2–3–4–?–?, is indicated. At least for the small species mentioned the phalangeal formula could be tentatively written 2–3–4–5(4?)–3.

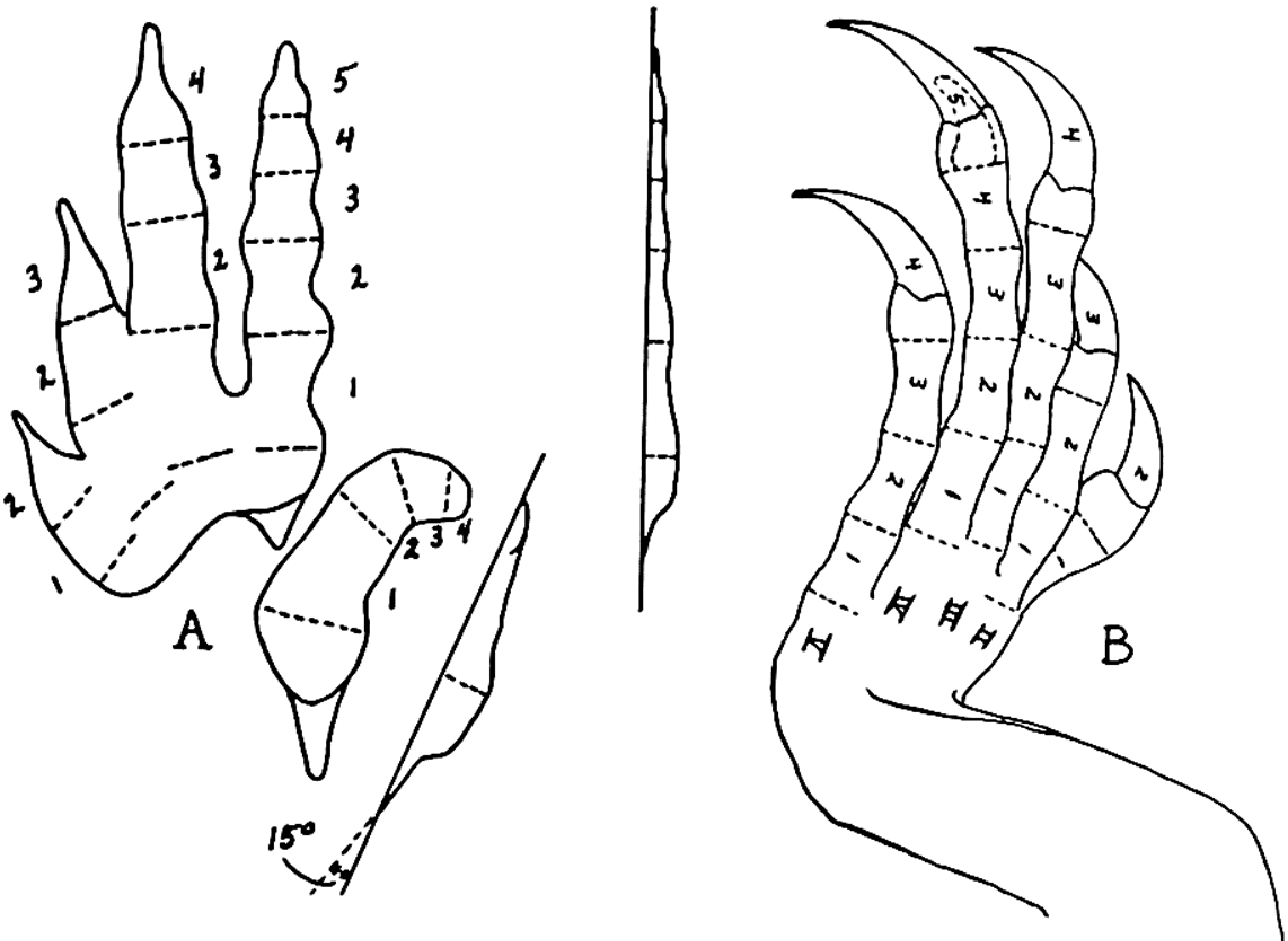

Fig. 36. *A*, probable position of skeletal joints in the pes of *Chirotherium minus*, with lateral profile shown for impression of digit IV and V; *B*, position of skeletal joints in the pes of an iguana. × ½.

The development of extensive digital pads in large chirotheriids obscures most indications of the phalangeal formula. It is impossible to tell whether a marked reduction in the relative length of pes digit IV means a reduction from 5 phalanges to 4 or fewer. The chances are it does not. Likewise it is impossible to tell whether a reduction in the importance of the phalangeal part of pes digit V means a similar reduction of phalangeal segments. The evidence indicates that except for minor variations in the terminal phalanges of manus and pes digit V, the formula is constant among chirotheriids.

In summary, the essentially reptilian character of the phalangeal formula of chirotheriids as established by Soergel is valid although derived by him mainly from a generalized assumption. The unpadded feet of certain small chirotheriids afford a more positive indication of the phalangeal formula. Inferences from the heavily padded digits of large chirotheriids can be made only on the basis of information supplied by the small species. Exception is taken here to

the reconstructed position and proportion of phalanges in *C. barthi* by Soergel (1925). The metatarsal-phalangeal and terminal phalangeal joints were given an unnatural distal position relative to the foot impression.

The phalangeal formula, as determined by positive methods from small chirotheriids, is: manus 2–3–4–5(4?)–3, pes 2–3–4–5–3(4).

The more obvious structural characters, skin, claws, and phalangeal pads, have been discussed first, then the phalangeal formula because it requires an interpretation of foot structure at variance with previous work. Remaining features of the chirotheriid foot can best be treated together.

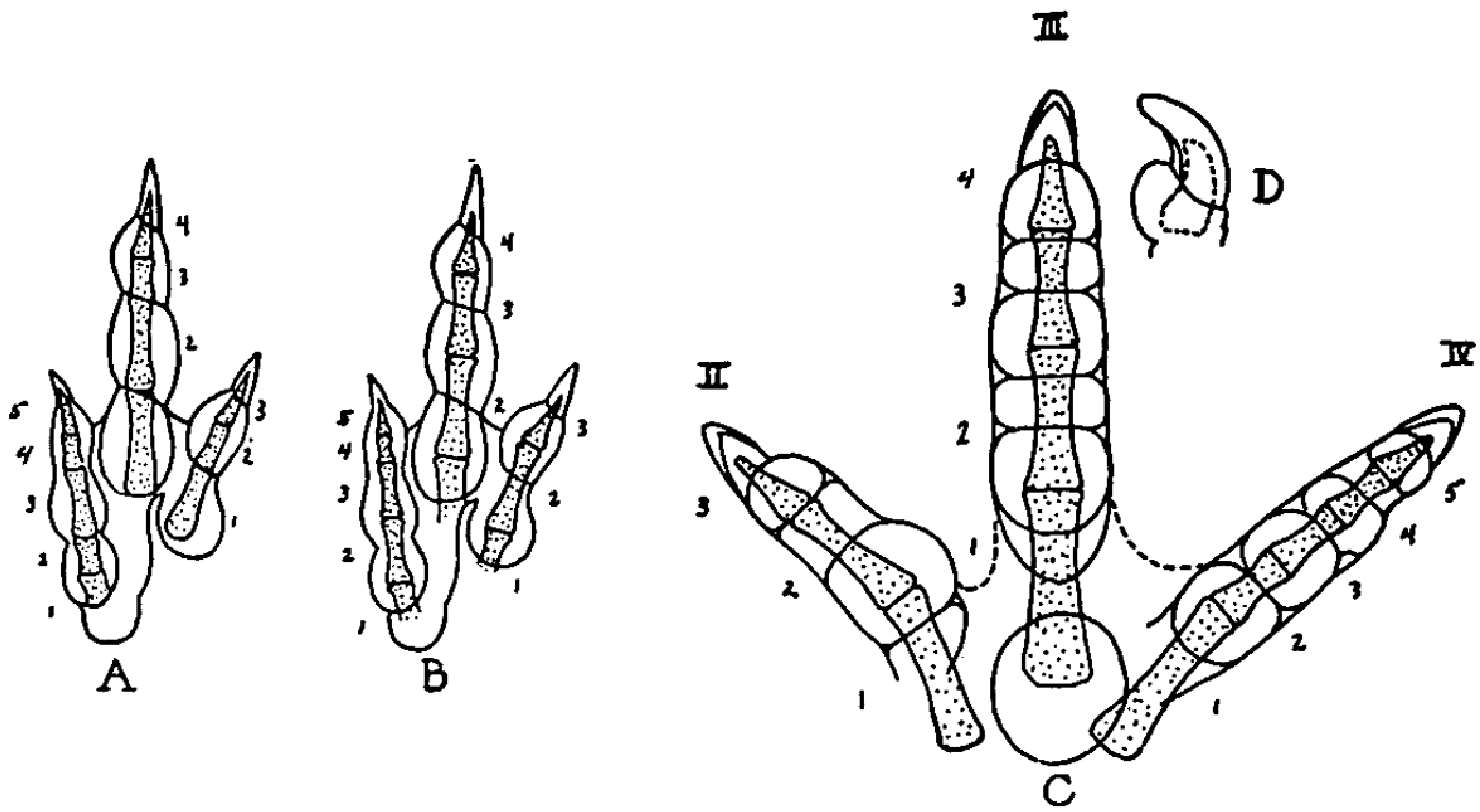

Fig. 37. *A*, reconstruction of phalanges in pes of *Grallator cursorius* by Lull, 1904, fig. 12; *B*, as reconstructed here; *C*, relation of the phalanges to the footprint of a domestic turkey; *D*, relation of ungual phalanx to horny claw and to terminal plantar pad.

MANUS

In the manus of primitive forms the digits are relatively long and slender. Digit IV is already shorter than III in contrast with the pes. Digit V is relatively large and independent of digit group I–IV. Appreciable flexibility of this digit is noted in *Chirotherium minus*. Passing through intermediate stages we find that in larger forms, particularly the small-manus species, the digits are very short and broad, the free length in group I–IV being somewhat less than the communal length (hypex to base). The fifth digit seems to have lost its independence and is appressed closely to digit group I–IV. The manus has the appearance of a hooflike organ suited only for walking. A grasping function seems possible only for the manus of small primitive species. In spite of its relatively small size it is regularly present in the trackway. Thus it appears that a basic trend toward bipedalism among chirotheriids was arrested, at least in larger forms, and the manus continued to function solely in a quadrupedal gait.

The character of the metacarpals must be largely inferred from what is known of the metatarsals. Metacarpal ridges are never seen in the deep im-

pressions, but from the disposition of digits and the incisive character of the posterior border of digit group I–IV we are safe in assuming a relatively steep inclination of the metacarpals compared with the metatarsals. The difference was most apparent in forms with a semiplantigrade pes. There is never any indication of a prone metacarpus V.

PES

The pes is basically digitigrade with metatarsals inclined at a moderately low angle to the ground. Among small-manus forms and giant forms generally the pes appears to be semiplantigrade, with considerable load carried by a nearly prone metatarsus V.

Primitively, digit group I–IV is much longer than broad and digit IV is as long as III. In addition the progressive increase of length from I to III is marked. Through intermediate stages a point can be reached where the length of group I–IV hardly exceeds the breadth and digit IV is reduced to less than the length of II. In apparent correlation there is a corresponding increase in the weight-carrying function of metatarsus V. Nearly half the weight borne by the pes in the small-manus species is carried by a large ovoid pad probably coextensive with metatarsus V. In contrast, only the distal end of metatarsus V is so used in primitive *Chirotherium minus*. This species is the only chirotheriid known to walk at times with all the weight borne by digit group I–IV. The fact that pes digit V may completely fail to impress, as illustrated by the American material, has resulted in a general misunderstanding of the species in Europe. Lydekker (1890) concluded that *C. minus* Sickler was a tetradactyl form, hence not a chirotheriid.

In effect, most of the large chirotheriids tended to "rock back on their heels" rather than to come up on their toes.

The phalanges of digit V constituted an awkward lateral protrusion at best. There is no evidence that any were ever lost although the main function of support seems to have passed over to the metatarsus. In some species, expansion of the metatarsal pad apparently engulfed the proximal phalangeal row, thus reducing its free length. The utility of such an organ is not easily understood. Originally it may well have had a grasping function as suggested by Soergel. In any event its conversion to a propping function seems to have been something less than successful. The function of support was localized about the metatarsus, leaving the phalanges to a secondary if not useless role. Whether or not the phalanges acted as an antiskid device while the animal was traversing soft mudflats is speculative. Perhaps the laterally directed phalanges originally functioned as a lateral prop which gave the chirotheriid walking gait a better balance.

METATARSALS

The sharply incised posterior border of digit group I–IV gives positive proof of the distal extension of metatarsals I–IV relative to each other. Obliqueness of the border in primitive forms indicates a lacertoid succession of length in which metatarsus IV is as long or longer than III. Shortening of metatarsus IV

is correlated with shortening of its phalanges. In most chirotheriids the posterior border of digit group I–IV is convex anteriorly in a manner indicating a transverse arching of the inclined metatarsals. In the giant species *C. rex* and *moquiensis* a transverse arch is apparently lacking.

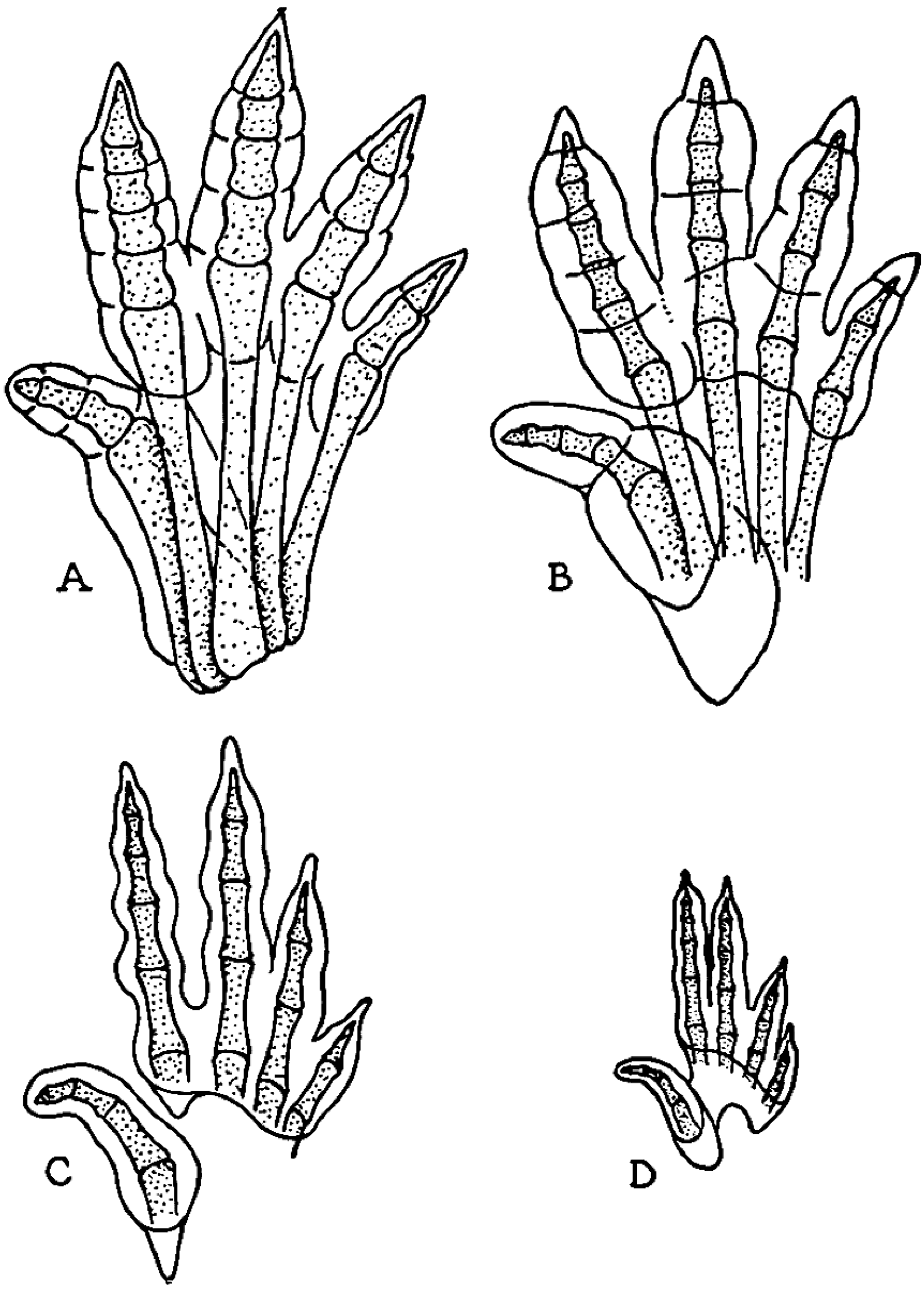

Fig. 38. *A* and *B*, comparison of reconstructions of pedal skeleton of *Chirotherium barthi* by Soergel (1925, fig. 29) and Peabody, respectively; *C*, pes of *C. minus* with reconstructed skeleton; *D*, *C. diabloensis*.

Casts of deep pes impressions of some species occasionally show converging ridges underlying the metatarsals. Each ridge originates from the bulge of the metatarsal-phalangeal joint and passes out proximally into the recording surface (fig. 36, *A*). In this manner the probable length and posture of metatarsals I–IV are indicated fairly well. The ridges converge proximally toward the tarsal region which in some species forms a definite heel. Soergel has found that metatarsals I–IV were inclined 10–20 degrees in *C. barthi*. For American examples of *C. minus* a minimum inclination of 15 degrees is indicated. Both values must represent a minimum angle since the pes impressions showing inclination of metatarsal ridges are infrequent in the trackway. Metatarsals I–IV

probably operated most of the time at some steeper angle. Occasional absence of the impression of pes digit V in *C. minus* indicates a minimum angle of inclination for metatarsals I–IV substantially greater than 15 degrees. Probably the angle of inclination was less than the values noted above in large forms with a semiplantigrade pes. This is indicated by the nearly prone position of metatarsus V.

The character of metatarsus V must be largely inferred from the character of the pad associated with it. In primitive *C. diabloensis* the slender digit V usually gives no indication of the separate skeletal components. Occasional deep impressions show a faint indication of the metatarsal-phalangeal joint at the point indicated in fig. 38, *D*. There is no sharp change of direction at the joint as noted in *C. minus* or *barthi;* rather, the metatarsus and phalanges functioned as an arc-shaped series of elements. By contrast the metatarsal-phalangeal joint in *C. minus* was the locus of pressure and the inclined metatarsus met the horizontal phalangeal series at an obtuse angle, about 140 degrees. This can be demonstrated in deep impressions which show a narrow metatarsal spur leading upward and backward from the rounded pad at the metatarsal-phalangeal joint (fig. 36, *A*).

The shape of the metatarsus appears to have been relatively long and slender in *C. minus*, perhaps similar to *Euparkeria* but with the proximal end underlying metatarsus IV. The exact shape of the proximal end is conjectural. A broad metatarsal spur leading proximally from the metatarsal-phalangeal pad in *C. barthi* is proof that the metatarsus was heavy and broad proximally according to Soergel. Assuming that this is correct, the metatarsus must have been even more massive in the semiplantigrade pes of other species. In the semiplantigrade pes the metatarsal pad apparently extended proximally to a tarsal heel and was so thick and massive as to conceal any skeletal detail; this supports Soergel's interpretation that the heel marked the proximal end of the metatarsals.

In all chirotheriids the metatarsal bundle was probably arched at its proximal end, with metatarsus V having a position under metatarsus IV. In this position it was utilized in some chirotheriids as a support for much of the weight borne by the pes. A topic which has not been considered before in the reconstruction of *Chirotherium* is the orientation of metatarsus V about its longitudinal axis. The phalanges of digit V operated in a horizontal plane rather than in the vertical plane of digits I–IV. This suggests that metatarsus V as well as its phalanges were rotated about 90 degrees laterally from the position of digit III.

The metatarsals were long relative to the phalangeal series as in pseudosuchians generally but the length reconstructed for *C. barthi* by Soergel is excessive, as demonstrated earlier (fig. 38, *A*, *B*). It so happens that digits I–IV of *C. barthi* are not particularly reduced in length. However, they are reduced in small-manus chirotheriids such as *C. marshalli* and the metatarsals may have been proportionately long to a degree approaching that interpreted for *C. barthi* by Soergel.

Study of the pedal anatomy suggested by the chirotheriid footprint makes

possible a reconstruction of the foot as it may have appeared in life. The pedes of *C. diabloensis*, *minus*, *barthi*, and *marshalli* are drawn here, all of the same size, principally to illustrate the character of the peculiar fifth digit and the probable posture of the foot (fig. 40).

TAIL

The presence of a long balancing tail is satisfactorily demonstrated for *Chirotherium* by Soergel despite the fact that the European trackways with which he dealt showed no associated tail marks. The Moenkopi trackways do contain several such records which substantiate Soergel's conclusions and add somewhat to our understanding of the chirotheriid body form.

It is perhaps significant that the most primitive chirotheriid, *C. diabloensis*, shows the most frequent occurrence of tail marks. Since it is the best represented of all the Moenkopi species, such marks, it must be admitted, would most likely occur. The single occurrence of a tail mark associated with a trackway of the much larger *C. barthi* is the only one known. For both species it is clear that a long tail, as determined by Soergel, was present. It was long enough to trail gracefully behind and in the marks cited actually dragged on the ground for short distances in a manner suggesting habitual carriage near the ground. None of the tail marks coincide with the midline; instead, they appear to be part of an undulate pattern which indicates an appreciable amount of lateral undulation of the body associated with the alternate pace of the walking gait. The indication of lateral undulation seems to support Soergel's contention that the walking gait of *Chirotherium* was not the perfected one of quadrupedal or bipedal dinosaurs. Herein may lie the reason why chirotheriids were essentially quadrupedal although showing strong bipedal tendencies in the marked reduction in size of the manus. The fact that chirotheriids were fully quadrupedal in spite of the small manus would suggest that Soergel's reconstruction of *C. barthi* (pl. 36) appears to be too far advanced toward bipedality.

The gait probably varied in different chirotheriids, being conditioned most certainly by differences in the structure of the postcranial skeleton. Primitive *C. diabloensis* apparently had the least perfected gait of all, as indicated particularly by the relatively wide trackway pattern, turned out pes, and undulate tail movement. On the other hand, *C. minus* was a long-limbed form with a narrow trackway and steeply inclined metatarsals although the foot plan was otherwise primitive. The specialized small-manus form, *C. marshalli*, had the narrowest trackway of all and apparently had perfected a walking gait approaching that of purely bipedal forms.

SKELETAL REMAINS POSSIBLY REPRESENTING *Chirotherium*

The most noteworthy attempts to relate *Chirotherium* to reptiles known from skeletal remains have been made by Soergel (1925) and by Huene (1936). Soergel has pointed out that the pes of *Euparkeria capensis* Broom (1913), an ornithosuchid pseudosuchian, could have made a chirotheroid track. We know that the ornithosuchids had a relatively small fore limb and showed a tendency toward bipedality, and therefore could have recorded a chirotheroid trackway

pattern. Especially corroborative of this view is the long metatarsus V, with its broad proximal end and well-developed phalanges, the long metatarsi I–IV, and the phalangeal formula 2–3–4–5–3 (fig. 39, *A*). However, Soergel was looking for the skeletal counterpart of *Chirotherium barthi* and does not seem to have considered the possibility that small-sized *Euparkeria* is more like certain

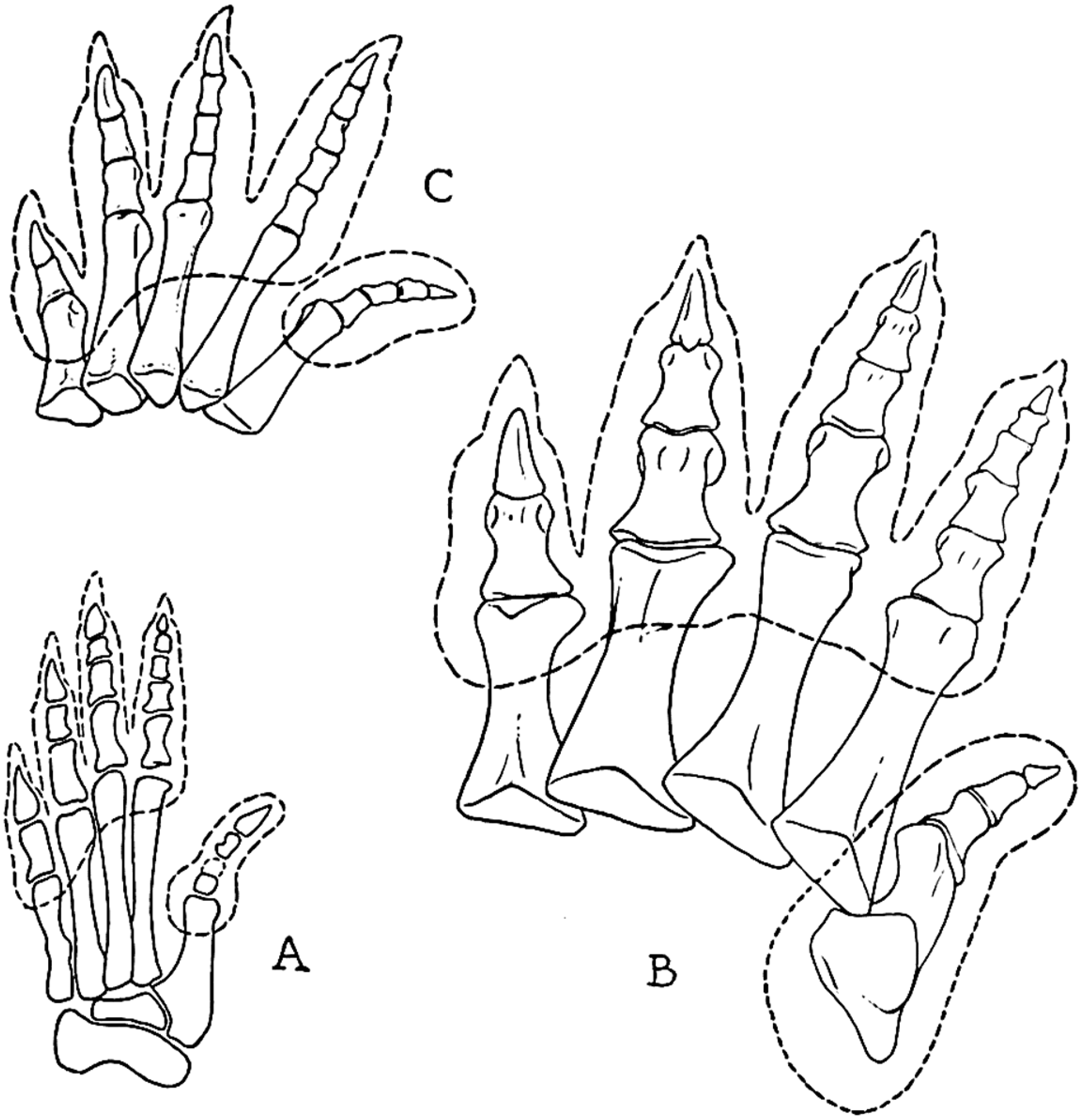

Fig. 39. *A*, pes of *Euparkeria* Broom showing outline of possible footprint, × 1; *B* and *C*, pes and manus of *Prestosuchus* Huene, showing outline of possible footprint (skeleton assembled from casts made by Huene), × ¼. Drawing by O. J. Poe.

small chirotheriids, particularly *C. minus*, which it resembles in the obliqueness of the metatarsal-phalangeal axis. As a matter of fact the distal extension of metatarsi reconstructed for this chirotheriid is very close to what exists in *Euparkeria*. The similarity holds also for the size of claws on digits I–IV and for the relative length of these digits. *Euparkeria* seems to present the strongest evidence for including the chirotheriids with the dinosaur-like pseudosuchians as represented by the Ornithosuchidae.

Huene presents the reconstructed skeleton of a large pseudosuchian, *Prestosuchus chiniquensis*, from the Triassic (Keuper) of Brazil. The conclusion is made that although *Prestosuchus* does not exactly fit *Chirotherium* (*C. barthi*),

both nevertheless belong to the stagonolepid pseudosuchians. I have been able to set up a duplicate cast skeleton of the manus and pes of *Prestosuchus* which was exchanged with the Museum of Paleontology by Huene. Although the resulting structure (fig. 39, *B*, *C*) may be incorrect in some details, it is possible to draw certain significant conclusions about the possible relation between *Prestosuchus*, the skeleton, and *Chirotherium*, the footprint. First of all, the skeleton is of a large reptile comparable to the largest known chirotheriid, and the manus, while greatly reduced in size, is large enough to compare with the large-manus chirotheriid, not with the small-manus group. In spite of a general similarity, the ways in which the skeleton does not "exactly fit" *Chirotherium* pose serious objections to Huene's conclusion.

Pes.—Digit group I–IV is extremely short and broad. The minimum width at the base (across the metatarsal-phalangeal axis) is in excess of 20 cm., not allowing for fleshy parts, and digit III, allowing for fleshy parts and including a horny claw, measures approximately 16 cm. Thus digit group I–IV is relatively much broader and shorter than any known chirotheriid except possibly *C. thuringiacum* Lilienstern (1938), which cannot be regarded as a true chirotheriid. This species has a very broad pes and a stubby, most unchirotheroid pes digit V. The *Prestosuchus* pes is also absolutely wider at the base of digit group I–IV than the largest chirotheriid. *C. rex* measures a maximum of 16 cm., which of course includes fleshy parts.

The claw phalanx is extremely heavy on digit I and graduates evenly downward in size to a very small phalanx on digit IV. Assuming that the horny claws showed a corresponding gradation, we have to recognize that such gradation is not found in chirotheriids where, although claw I may be long but narrow, claws II and III are the largest. Claw IV never is as small as the size indicated for *Prestosuchus*.

Metatarsus V has the broad proximal end to the hatchet-shaped metatarsus as in *Euparkeria*, and the phalanges apparently were capable of movement in a horizontal plane. However, the relative size of the digit is much smaller than required for the typically massive chirotheroid impression. The digit tip hardly reaches the metatarsal-phalangeal joint of digit IV, even allowing for the extension of a horny claw. The metatarsus does not seem long enough, large enough, or expanded enough laterally to have supported the massive pad of the giant chirotheriids. However, this last relation could be misinterpreted: one would have difficulty in divining the expanse of the huge cushioning pad of the elephant foot from skeletal evidence alone.

Manus.—Digit IV is the longest, even allowing for a relatively shorter claw to correspond with the small claw phalanx. In all chirotheriids this digit is noticeably shorter than III, which is always the longest, and no longer than II. The phalanges of digit V seem to have been capable of movement in a more or less horizontal plane, but the proximal end of the metacarpus indicates a parallel alignment with the other metacarpi rather than the somewhat oblique alignment necessary to bring the phalanges to the chirotheroid position. Also the phalanges appear to be relatively slender, considering the stubby, wide digits of giant chirotheriids.

The complete skeleton of *Prestosuchus* as mounted by Huene does not appear to indicate the degree to which chirotheriids had shifted the body weight to the hind limbs. On the other hand, I feel that Soergel's reconstructed figure of *Chirotherium barthi* has gone too far in this direction.

From the foregoing comparison it is concluded that the stagonolepid, *Prestosuchus*, does not represent any known chirotheriid. The ornithosuchid foot as represented by *Euparkeria* presents a skeletal structure more nearly in accord with that reconstructed from chirotheriid footprints.

EVOLUTION OF THE CHIROTHERIIDAE

Description of species and discussion of the structure of *Chirotherium* have touched upon characters which suggest evolutionary trends among the Chirotheriidae; nevertheless, an actual evolutionary series of species is not clearly shown. Evolutionary trends suggested by the structural diversity among chirotheriids are:

1. A general shortening of digits and development of specialized phalangeal and metatarsal pads.
2. A relative reduction of pes digit IV and its metatarsus.
3. A relative reduction of the phalangeal part of pes digit V with a transfer of the locus of pressure to the metatarsal.
4. A change from digitigrady to plantigrady in the pes, associated with gigantism, in which half the weight borne by the pes was transferred to the fifth metatarsal.
5. Associated with item 4 is a general regression from an original tendency toward bipedalism, in which the manus loses its grasping function and develops into a hooflike organ. The manus is most hooflike in the small manus forms.
6. A divergent, but perhaps significant trend toward long-legged, agile forms with a more efficiently propped foot, as in *C. minus*.
7. A development in a few chirotheriids of a purely bipedal gait (not clearly demonstrated by known trackways).

The family Chirotheriidae, as a whole, seems to represent an important unit in a poorly known complex of early Triassic reptiles, some of which gave rise to the varied dinosaurs of later times. As Soergel suggests, the family represents a sort of "blind alley" in the development of the dinosaurs. Large chirotheriids such as *Chirotherium rex* surely represent end forms and could not have evolved into any known type of dinosaur. Soergel also suggests that the Chirotheriidae evolved from quadrupedality to complete bipedality within its known history. The suggestion is based on the belief that chirotheriids in the English Keuper,[5] as represented by the small-manus species *Chirotherium beasleyi* (= *C. storetonense* Soergel) and the completely bipedal species *C. bipedale*, were further advanced toward bipedality than earlier Bunter species as represented principally by *C. barthi*. It is demonstrated in the present paper that small-manus species also occur in the German Bunter. In the Lower Moenkopi a small-manus species, *C. coltoni*, is demonstrated to be essentially

[5] See footnote 1, page 301.

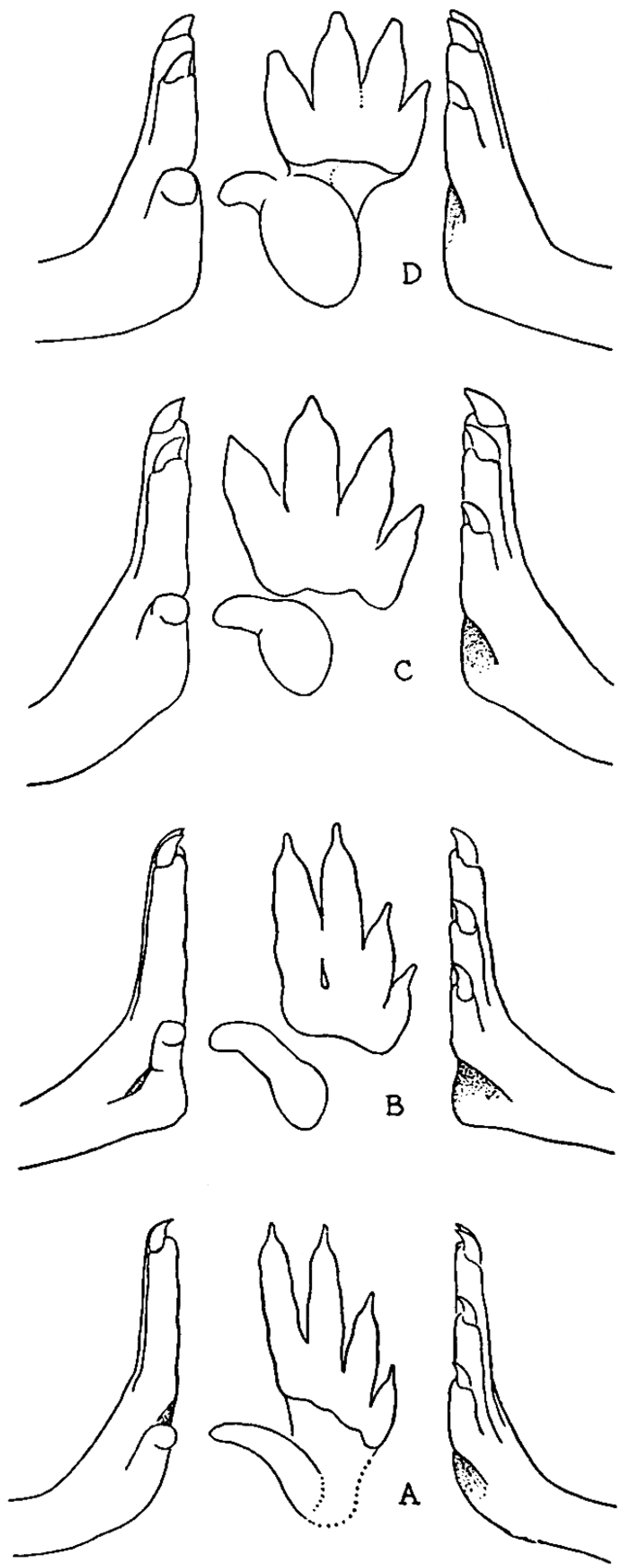

Fig. 40. Reconstructed pedes of *Chirotherium: A–D, C. diabloensis, C. minus, C. barthi, C. marshalli,* respectively. Lateral view (left), plantar v. (middle), median v. (right). For relative size, see fig. 33.

contemporaneous with a species of primitive structure, *C. diabloensis*. Also, the existence of a purely bipedal species in the Lower Moenkopi is suggested by a single trackway (cf. *Chirotherium* sp. indet.).

The Chirotheriidae apparently originated in pre-Moenkopi time from a group of pseudosuchians which showed a strong tendency toward bipedality, and it seems apparent that the awkward-footed *Chirotherium* represents an early but unsuccessful attempt to produce a bipedal reptile. The family split early into subgroups, as indicated by early contemporaneity of large-manus and small-manus species. Both groups developed gigantic forms. Possibly the latter group developed a few purely bipedal forms, but the general tendency was away from the initial trend toward bipedality.

An exception to this general tendency is found in *Chirotherium minus*. As mentioned earlier, this form was misunderstood in Europe because of the habit of walking at times entirely on the first four digits of the pes, this in spite of a robustly developed fifth digit. The reptile was of medium size, long-limbed, perfected in its walking gait as shown by the long striding and narrow trackway, and the pes was propped up more by the fifth digit than in any other chirotheriid. It is possible that continued and exclusive use of pes digits I–IV would cause the then useless fifth digit to degenerate rather quickly. The resulting pes structure would be very close to that known for early dinosaurs such as *Anchisaurus*. In addition the manus of *C. minus* possessed an extremely independent fifth digit and the other manus digits were long and flexible, thus making an excellent grasping organ. If consideration is given to the probable diversity occurring in dinosaurian ancestral lines, it is not difficult to regard the reptile represented by *C. minus* as a possible ancestor of some of the later dinosaurs.

The characters of *C. minus* are doubly interesting for the light they throw on the evolution of the cursorial foot of dinosaurs and birds. It is entirely possible that the advanced digitigrady of the dinosaur and bird pes was originally initiated by the propping function of a strongly developed fifth digit. As indicated by *C. minus*, digit V may have lost its function altogether when the metatarsal bundle became inclined at some critical angle. The awkward prop of the *C. minus* pes and the seemingly more efficient, rotated prop of the *Rotodactylus* pes strongly suggest this probable step in the evolution of the cursorial pes of dinosaurs and birds. Granted that this might be true, then it would seem that the rotated *first* digit in the pes of certain dinosaurs and birds is a secondary adaptation for a propping or grasping function. Loss of a functional fifth digit in the ancestors of dinosaurs and birds may have brought about the later use of digit I as a propping or grasping organ.

ENVIRONMENT

Wide range in size and structure within the Chirotheriidae indicates that the family successfully invaded a number of environmental situations and was probably the dominant, terrestrial vertebrate of Moenkopi time. Geologic occurrence of the trackways indicates that chirotheriids inhabited the valleys of streams subject to much fluctuation of water level. Orientation of the track-

ways on mudflats originating from the fluctuations is generally monaxial, that is to say, where several trackways occur together they usually lead in one of two opposite directions. In at least two occurrences, Meteor Crater and Moqui Wash, some trackways lead upstream, others lead downstream. The trackways, with few exceptions, indicate that the reptiles were on their way from one place to another and did not loiter on the mudflats. This is usually true for vertebrate trackways seen on recent fluvial mudflats. A fluvial mudflat, in itself, offers a direct path for travel but provides little or no food or cover.

Soergel suggests that the sharp, strong claws of certain species of *Chirotherium* indicate carnivorous habits. Certainly there was a variety of animal food available. Possible sources are suggested by the tracks of small crustaceans and of many small, lacertoid reptiles which occur on mudflat surfaces with *Chirotherium*. Also, associated fluviatile deposits contain remains of ganoid fish and diverse types of amphibia. If Soergel is correct in his interpretation that sharp, strong claws indicate carnivorous habits, then the hooflike claws of certain large chirotheriids may well indicate herbivorous habits. A wide choice of vegetable food is not indicated by fossil plants in the Moenkopi. Indeed, the evidence of a Moenkopi flora is so scarce as to arouse suspicion. Certainly a land supporting a diversified vertebrate fauna such as we know existed must have supported also a diversified flora. The few impressions of reeds and *Equieseta* discovered in Moenkopi strata must therefore represent a very small part of the Moenkopi flora.

SUMMARY

1. A fauna of amphibians and reptiles from the Lower Triassic is described from the trackways which they left in the Moenkopi formation of northern Arizona. The present study was preceded by an investigation of the trackways of many living amphibians and of several living reptiles. The investigation enables one to distinguish more clearly the trackway characters which portray the anatomy of the foot from those arising from differences in the recording surface and from motion of the animal. As far as possible the description of fossil trackways is based on the pedal anatomy interpreted from clear and undistorted footprints. A system of measurements is introduced in which the relative width of the trackway pattern is expressed in degrees (pace angulation) and is independent of linear measurements. The new term "hypex" is used to designate the apex of the reëntrant angle between digits.

2. Trackways of living vertebrates are diagnostic of the genus but not of the species; therefore, differentiation of fossil vertebrates by their trackways is of necessity on a generic level relative to living vertebrates.

3. The Moenkopi formation in the valley of the Little Colorado River between Cameron and Holbrook is fossiliferous below and above a generally median zone of gypsiferous shales. Pregypsum and postgypsum stages are referred to as the Lower and Upper Moenkopi, respectively. The trackway-bearing strata are of fluviatile origin. Trackways usually occur on desiccated mudflat surfaces comparable to recent fluvial mudflats. Crescentic eddy marks, called current indicators, sometimes are associated with vertebrate trackways.

Such occurrences show that species of *Chirotherium* usually traveled up- or downstream and not at right angles to the stream channels.

4. Correlation of the Moenkopi with the European Lower Triassic on the basis of vertebrate trackways is difficult. The large-manus chirotheriids, *Chirotherium minus* Sickler and *Chirotherium barthi* Kaup, which occur together in the Upper Bunter of Germany, occur separately in the Lower and Upper Moenkopi, respectively. And a small-manus chirotheriid, *Chirotherium marshalli*, from the Upper Moenkopi, seems most closely related to *Chirotherium beasleyi*, from the early Middle Keuper of England. A complete revision with some redescription of critical European chirotheriids may, in the future, resolve the seeming inconsistencies of distribution.

5. Trackways of Amphibia are rare in the Moenkopi although skeletal remains are relatively abundant. Several footprints from the Lower Moenkopi are assigned to the Capitosauridae largely on the evidence afforded by an articulated capitosaurid skeleton found at the same level as the footprints. The skeleton is reconstructed and found to be of salamander-like proportions, except for the elongate head, and to have well-developed limbs. Living salamanders and their trackways are used to reconstruct the probable tracks of a capitosaurid. The probable footprints in the trackway are then compared with the fossil footprints and found to be similar.

6. The geologic occurrence of the fossil footprints indicates that the capitosaurs lived in and around a river and at times crawled or walked over exposed sand bars. The capitosaurs did not venture onto the many mudflats traversed by a variety of reptiles.

7. Small footprints of lacertoid reptiles are more abundant in the Moenkopi than any other kind, yet very few clear trackways can be recognized. Five lacertoid trackways of poor quality are described: Three resemble *Akropus* Lilienstern from the German Bunter which is thought to represent a protorosaur; two apparently have rhynchocephalian characters although skeletal remains of this group are unknown in the Lower Triassic.

8. Living lizards and their trackways are used in the analysis of the fossil lacertoid trackways. Attention is called to the fact that in lacertoid trackways, unlike those of other tetrapods, the manus is always more clearly and more completely impressed than the pes. A "bipedal" trackway described by Huene (1935) is actually a lacertoid trackway which lacks a recognizable pes impression.

9. Small reptile footprints from the Upper Moenkopi having a backward-projecting spur were described but left unnamed by Brady (1935). Several subsequently discovered and complete trackways from the Lower Moenkopi are described here. The pedal anatomy, including skeletal elements, is reconstructed from particularly clear impressions. The spur represents the fifth digit rotated to the rear, where it functioned as a springy prop for the foot, particularly for the pes. Contours of the digit impressions indicate that the first phalanges were elevated along with the metapodials. This advanced digitigrade posture of the foot is correlated with a fairly narrow trackway pattern in which the feet point forward and the pes noticeably oversteps the

manus. The manus impression may or may not be present in the trackway pattern. Particularly fine impressions of the scaly plantar surface are described.

10. The reptile which made the spur-footed trackways was a slender, agile animal of dinosaur-like form tending toward bipedality; it represents a distinct family of Pseudosuchia and is perhaps related to the Ornithosuchidae; but it is unique in possessing a proplike fifth digit and a long fourth digit. The new genus *Rotodactylus* and the new family Rotodactylidae are proposed for the spur-footed trackways. One species from the Lower and two species from the Upper Moenkopi are described.

11. The pseudosuchian family Chirotheriidae proposed by Abel (1935) on the basis of Soergel's work (1925) on *Chirotherium* is redefined, and the long and devious history of the discovery and description of *Chirotherium* species is reviewed.

12. Review of previously described species of *Chirotherium*, mostly European, is undertaken, although the available written descriptions are often inadequate for the purpose. Soergel's important paleobiologic contribution (1925) introduces several new species of which the formal descriptions are contained in an unpublished work.

13. The new species *Chirotherium beasleyi* is proposed for the small-manus chirotheriid described by Beasley (1906, 1907) and Lomas (1907).

14. Eight species of *Chirotherium*, six of them new, are described from the Moenkopi formation, and their relationships are discussed. Tail marks are found for the first time in association with the trackway pattern of *Chirotherium*. Trackways of three species indicate a marked size range among individuals. Particularly fine impressions of the scaly plantar surface are described.

15. Previous diagnoses of the family Chirotheriidae and of the genus *Chirotherium* contain characters which pertain indiscriminately to several different taxonomic categories. These characters are allocated to the proper taxonomic categories.

16. The Chirotheriidae is divided into a large-manus group and a small-manus group. In each there are primitive, advanced, and giant forms. Evidence is not clear for a third group comprising bipedal forms.

17. The feet of living reptiles and birds are used in analysis of the foot structure of *Chirotherium*. Small primitive types lack specialized digital pads and as a result the position and dimensions of phalanges and metapodials are indicated in clear footprints. The reptilian phalangeal formula (manus, 2–3–4–?5–3; pes, 2–3–4–5–3[4]), is positively determined. Results of the analysis of pedal anatomy are embodied in reconstructions of the pes in four species.

18. The Chirotheriidae originated in pre-Moenkopi time from a group of pseudoscuhians which showed a strong tendency toward bipedality. The family split early into at least two subgroups both of which developed gigantic forms. An important evolutionary trend was a reversal of the initial tendency to become completely bipedal.

19. The foot structure of the Rotodactylidae and Chirotheriidae suggests that the cursorial foot of dinosaurs and birds passed through an early struc-

tural stage in which a digitigrade posture was initiated by the use of the fifth digit as a prop. Each of the two families illustrates a unique method by which the fifth digit was employed to elevate the foot.

20. The Moenkopi trackways represent a large and varied fauna consisting principally of reptiles. Since skeletal remains of reptiles are fragmentary and scarce, the trackways provide the only clear picture we have of the early Triassic history of North American reptiles, particularly the Archosauria.

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PLATES

PLATE 23

A, redbeds of the Moenkopi formation lying on Permian Kaibab limestone. View looking west from near the Flagstaff–Cameron highway opposite Gray Mountain (skyline). Navajo Indian encampment in the Kaibab valley. *B*, amphibian quarry in the Lower Moenkopi near Meteor Crater (skyline at left). Underside of sandy limestone lens in foreground preserved the trackway surface shown in fig. 21. Level at base of butte in middle background (arrow) produced trackway surface shown in figs. 16, 17, and in pl. 37. View looking south; photograph by S. P. Welles.

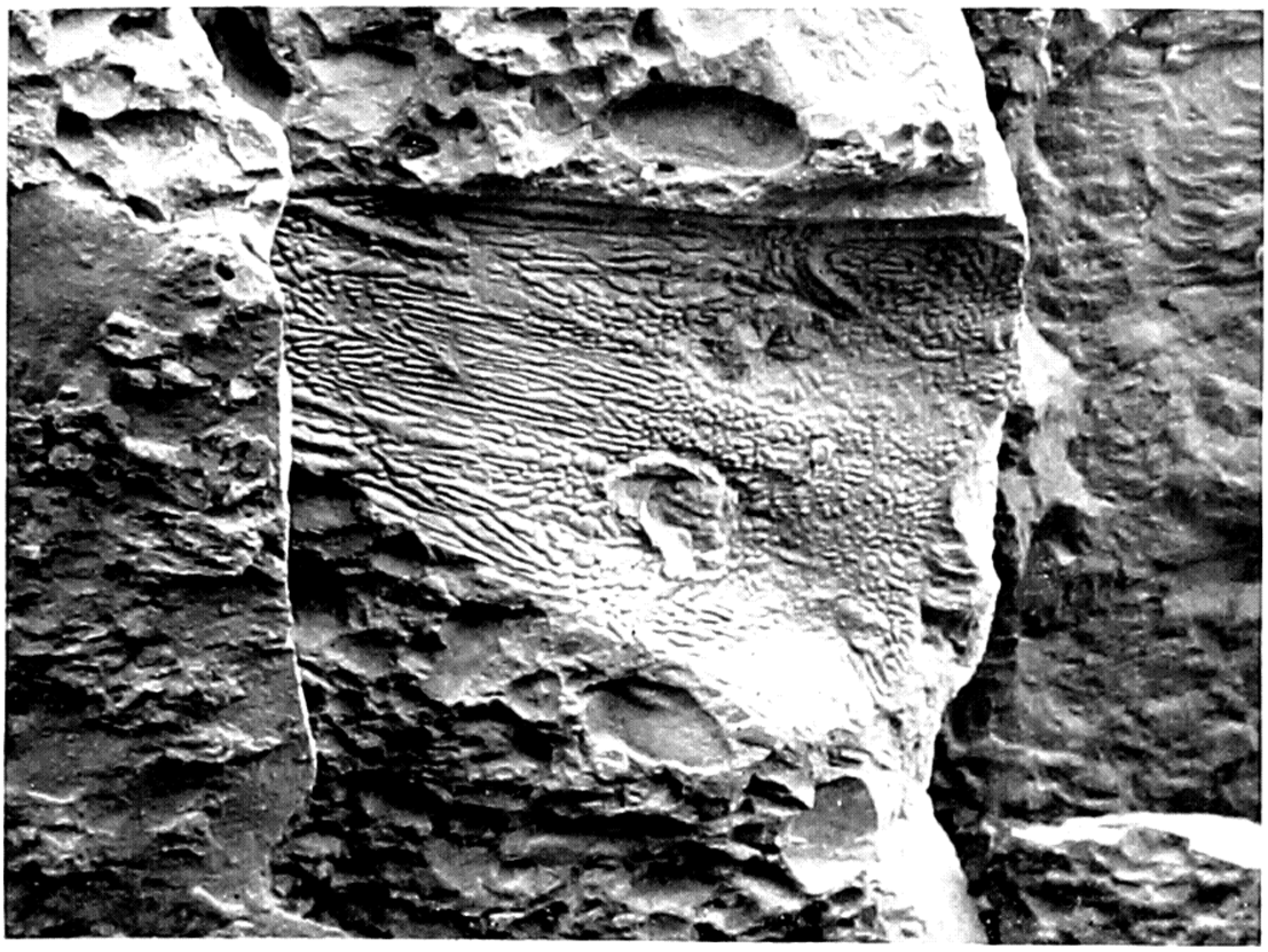
A

B

PLATE 24

A, impression of a capitosaurid skull associated with shale pebbles in a fluviatile foreset bed (in place), Lower Moenkopi of Moqui Wash. View looking up under ledge of cross-bedded conglomeratic sandstone. *B*, current indicator from a mudflat surface in the Lower Moenkopi of Meteor Crater. On left, sandstone cast of original current indicator showing where original shale pebble weathered away leaving a cavity. On right, latex rubber impression taken from the cast, showing original shape of flat pebble.

A



B

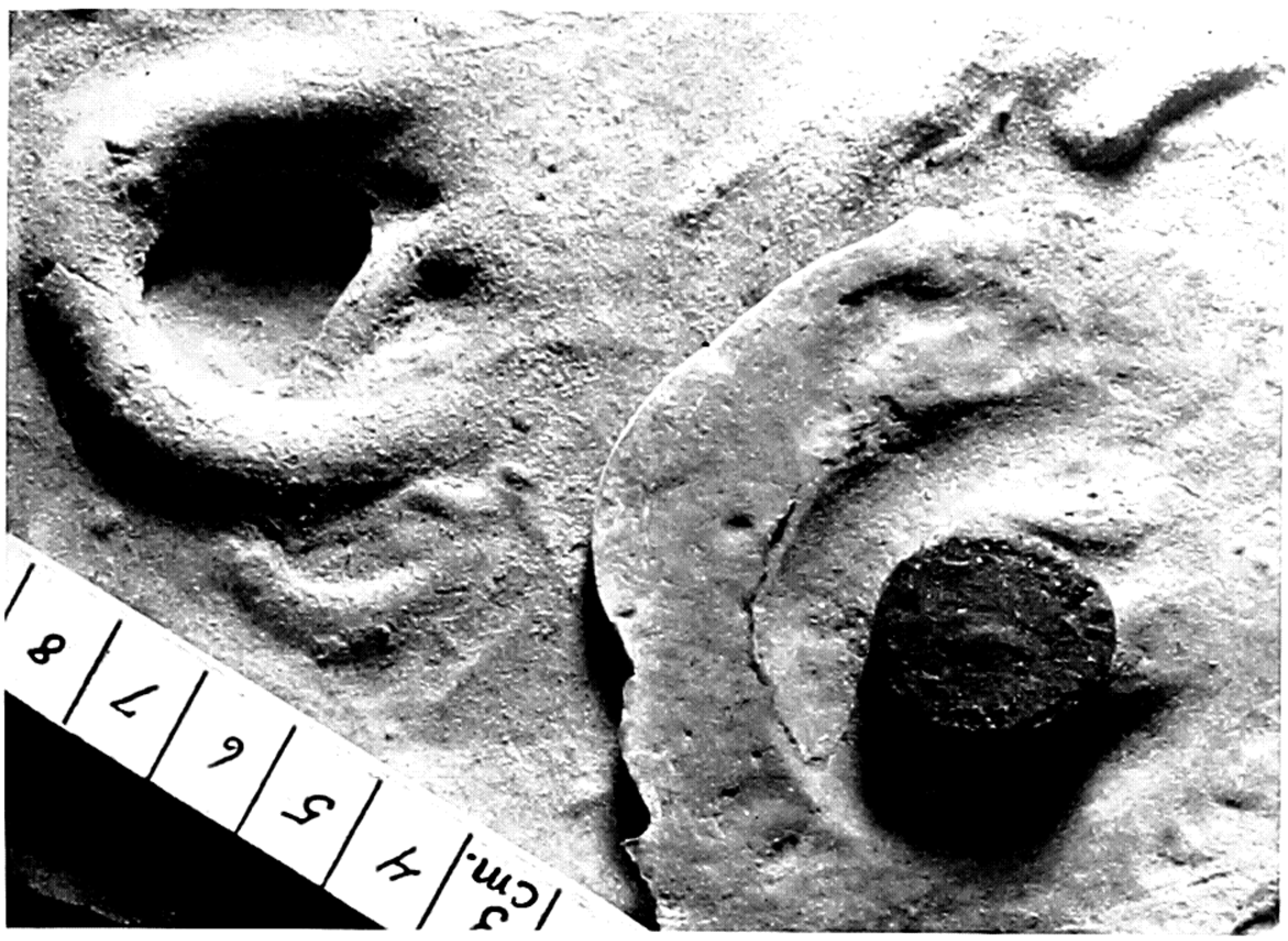
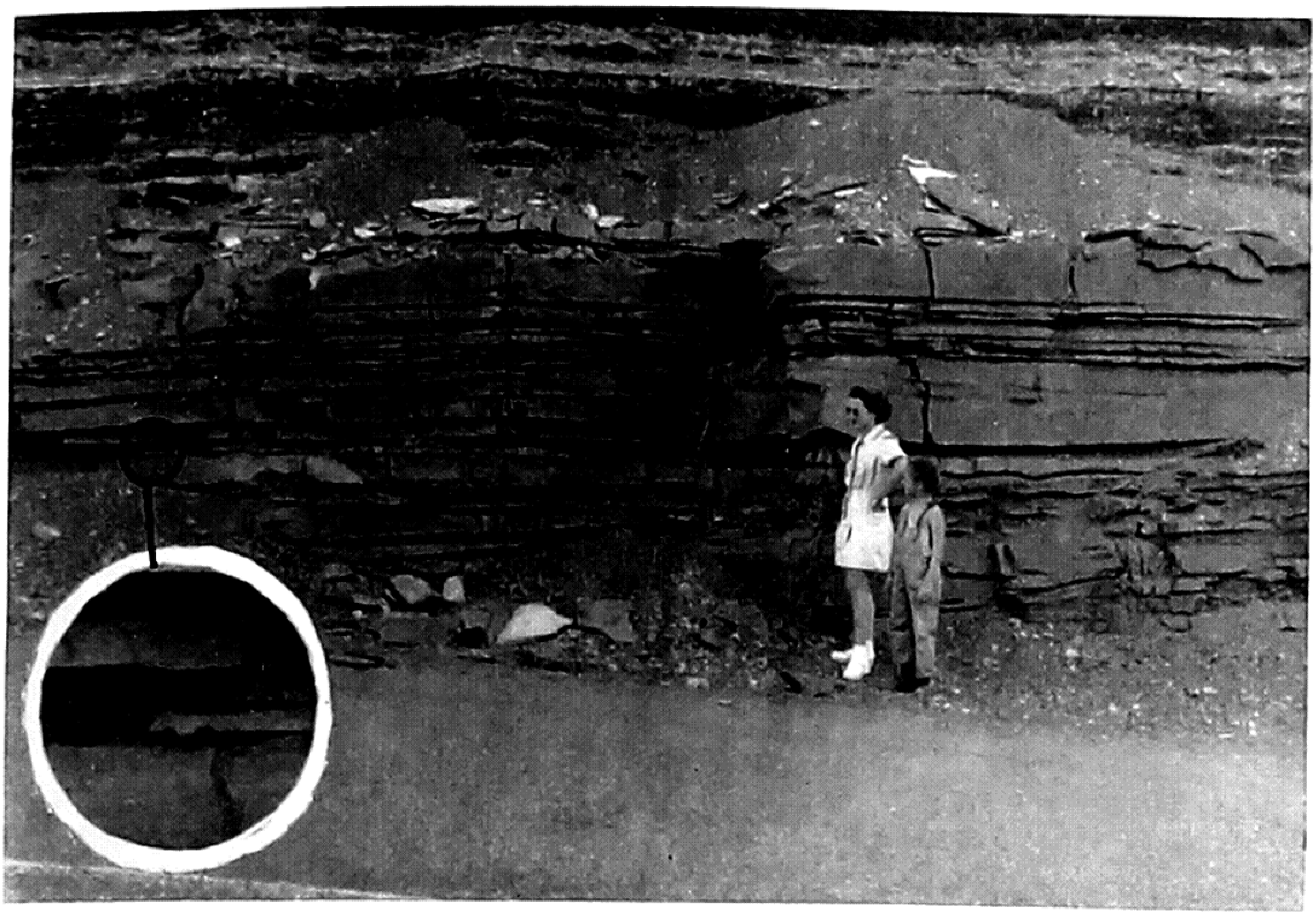


PLATE 25

A, section in Upper Moenkopi exposed in road cut on Flagstaff–Cameron highway. Channel sandstone, overlain by even-bedded shale, contains thin lenses of shale representing recurrent mudflat surfaces. Surface indicated by small circle contains many footprints (pl. 43). Insert shows cross section of *Chirotherium barthi* pes in place. *B*, underside of a ledge of sandstone (in place) which has cast the details of a Triassic channel bottom eroded in even-bedded shales. View looking obliquely upward under the ledge.

A



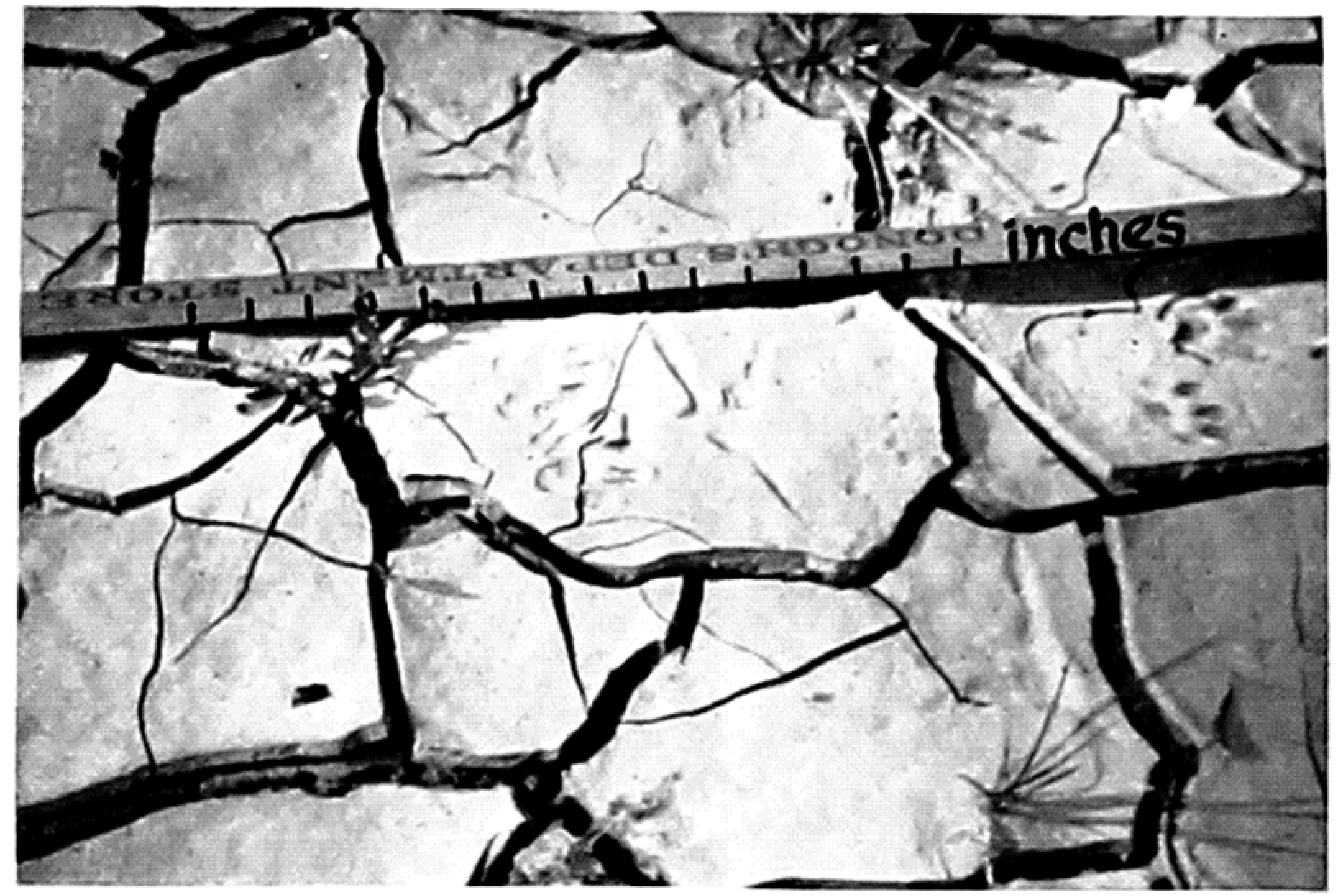
B

PLATE 26

A, mudflat on bank of the Russian River, California, in advanced state of desiccation. Note vegetation growing through cracks in the surface. *B*, small area of the mudflat showing tracks of a wading bird (bittern) and of a mammal (raccoon). Note looseness of individual plates of dried mud. *C*, plaster cast of crack system redeveloped in marl reclaimed from the fossil trackway surface of the amphibian quarry at Meteor Crater (fig. 21). The marl has remained unchanged, apparently since Triassic time. Mixed with water it made an excellent medium for recording trackways of living salamanders (pl. 28, *B*).

A

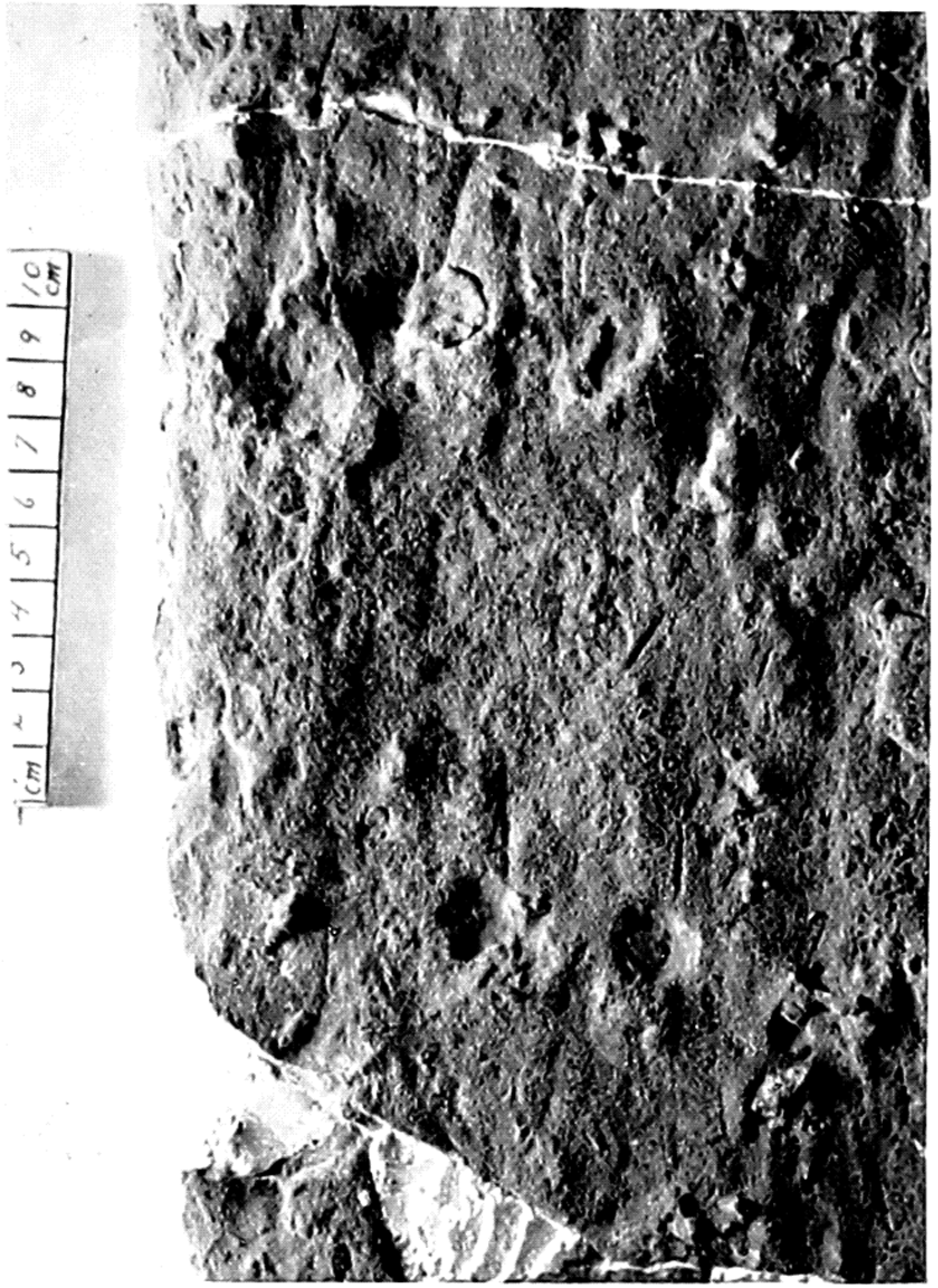
B



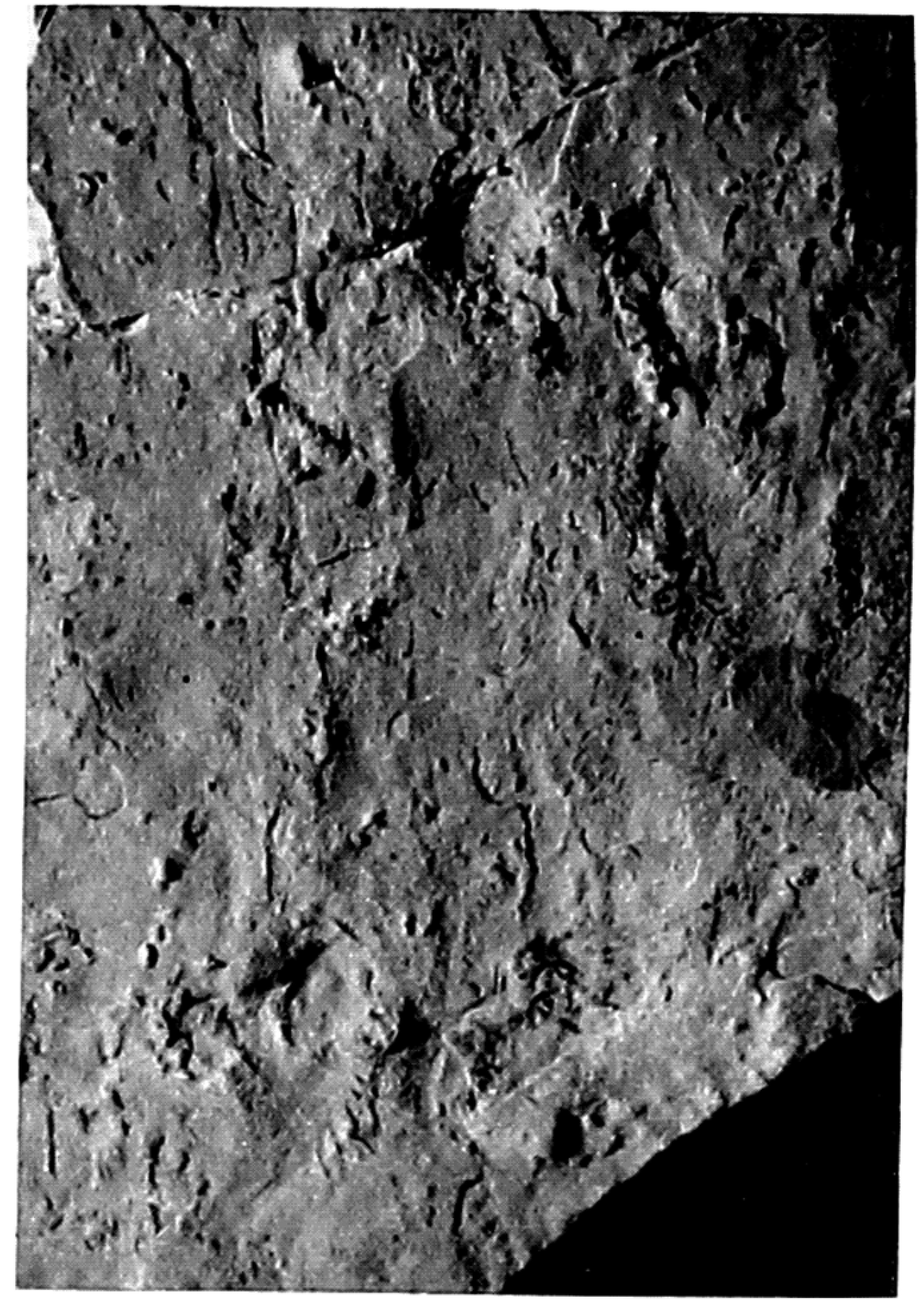
C

PLATE 27

Capitosaurid footprints from the Lower Moenkopi of Moqui Wash: *A*, no. 37759; *B*, no. 37760; diagram of impressions shown in fig. 9. × ½.



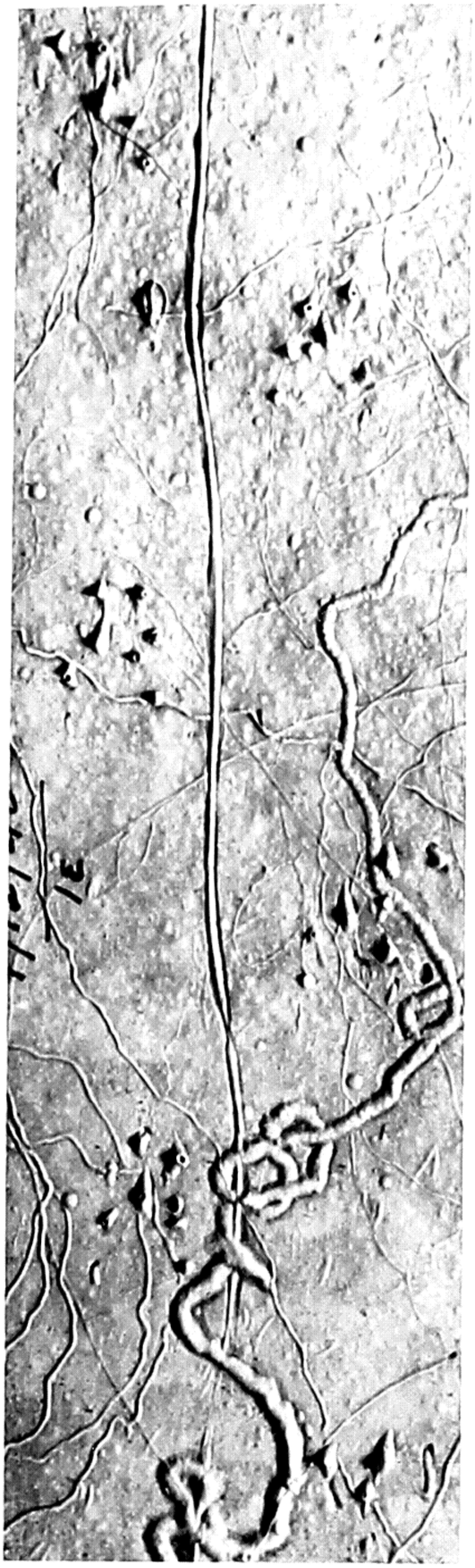
A



B

PLATE 28

Plaster casts of trackways of living salamanders: *A*, *Triturus torosus* recorded on a natural mudflat (note invertebrate trails); *B*, *Aneides lugubris* recorded on reclaimed Triassic marl from Meteor Crater. × 1.



A

B

PLATE 29

Trackways of five lacertoid reptiles from the Upper Moenkopi near Shadow Mountain. Arrows show consecutive manus impressions. Encircled isolated manus shows lowest range in size; note that numerous isolated footprints have been painted over. Trackway 1, no. 37343; 2, no. 37796; 3, no. 37797 (Group 2, cf. *Akropus* Lilienstern); 4, no. 37344; 5, no. 37795 (Group 2, rhynchocephaloid ?).

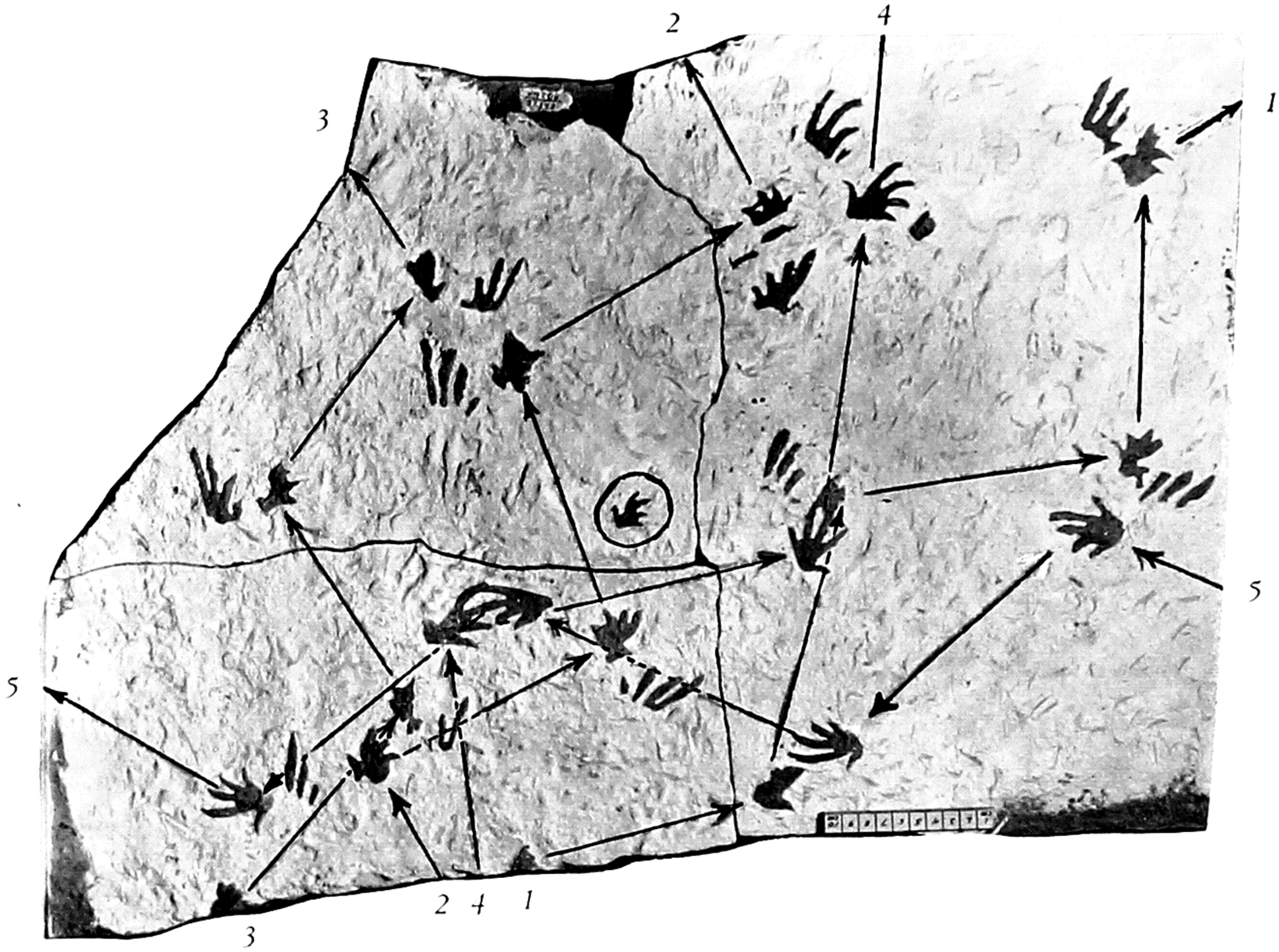
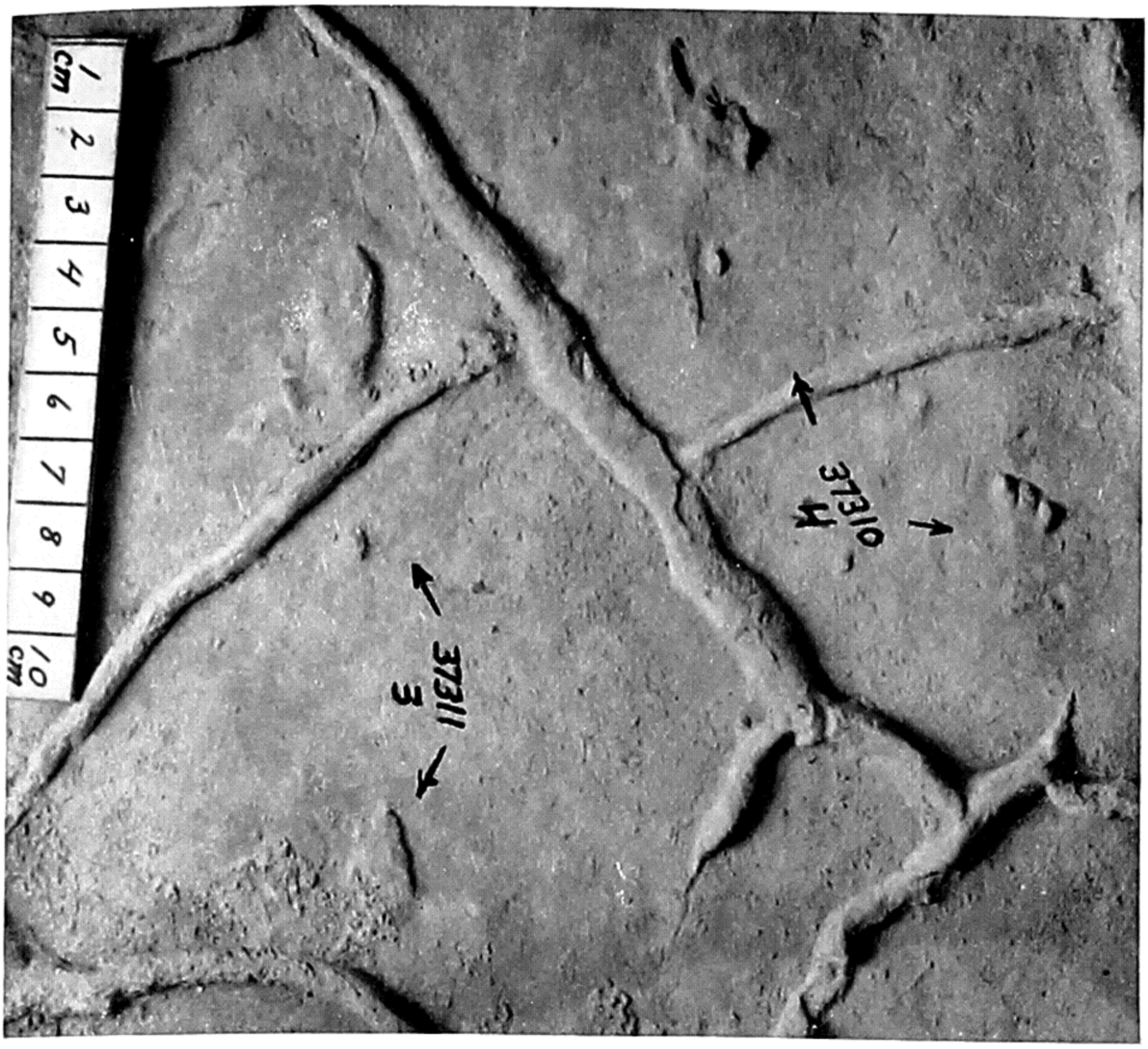
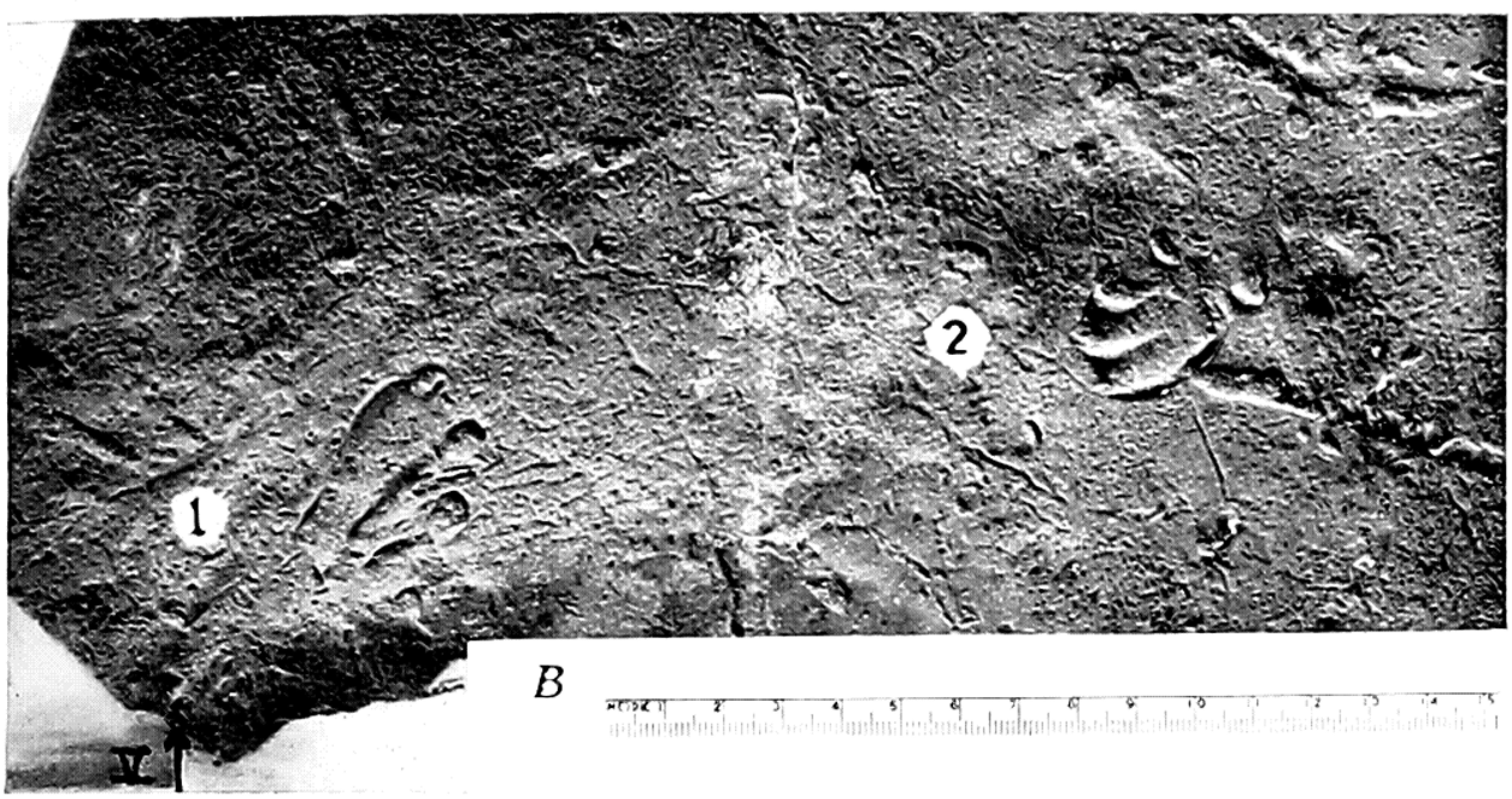

2
4
1
3
5
5
2 4 1
3

PLATE 30

A, *Rotodactylus cursorius;* photograph of surface indicated by rectangle in fig. 17, showing manus and pes from two different trackways representing different individuals; *B*, *Rotodactylus bradyi;* isolated pes (1) and manus (2). Mus. Northern Arizona no. G2.2614, photograph by L. F. Brady.



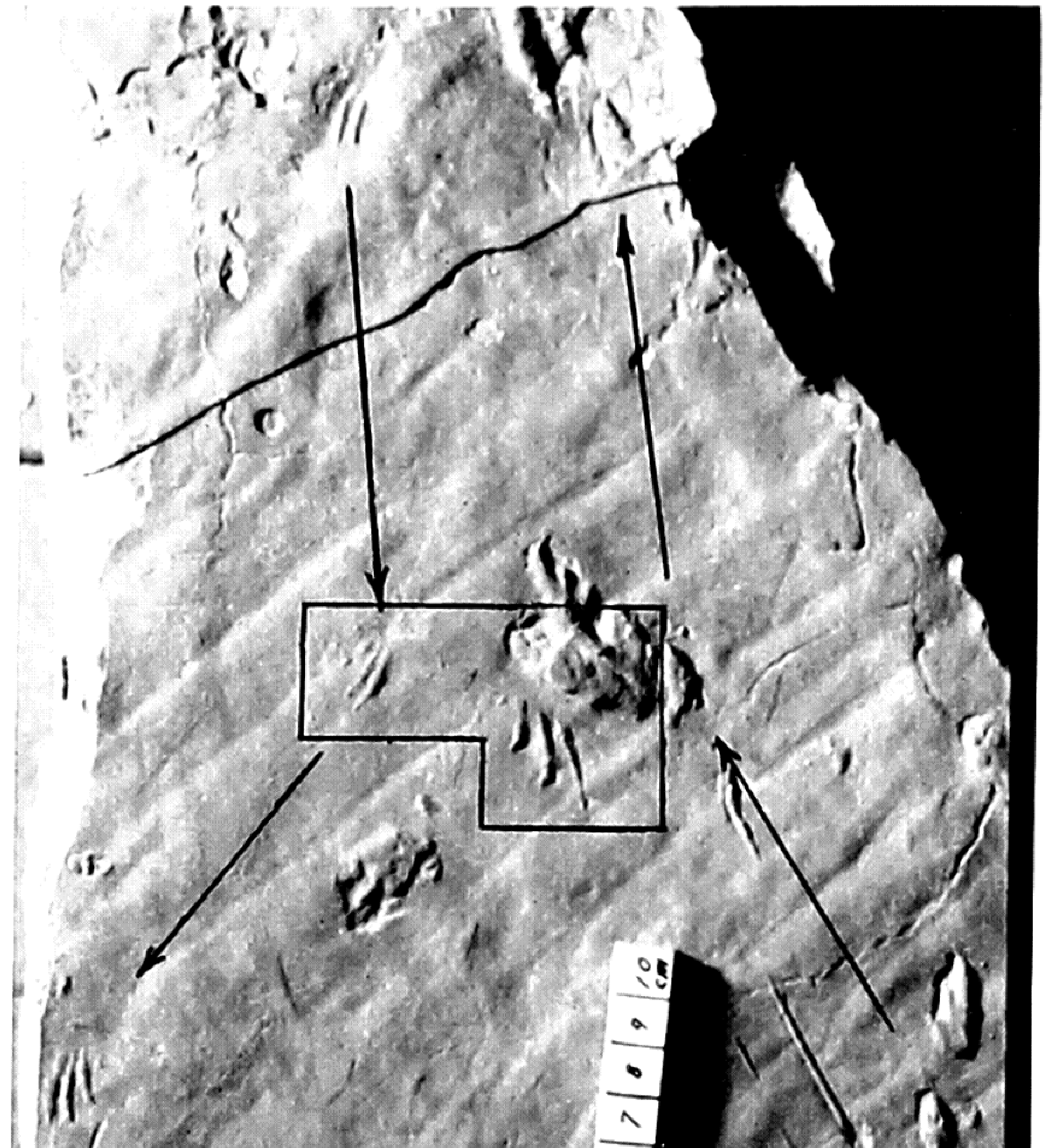
A



B

PLATE 31

Rotodactylus mckeei trackways from upper Moenkopi of Hurricane, Utah, loc. V4602: *A*, slowly walking individual; step 2 shown enlarged in pl. 32, *F*; *B*, running trackway of small individual. Pes of large individual occurs between steps 1 and 2 and in the corner of the ruled area. Arrows indicate consecutive manus impressions.



A B

PLATE 32

Rotodactylus mckeei: *A*, manus and pes of type; *B*, manus and pes of smallest indivdual; *C*, manus; *D* and *E*, pes, showing parts of the scaly plantar surface; *F*, manus and pes from trackway *A*, pl. 31, enlarged to show detail of the scaly plantar surface; *C–F*, shown in fig. 19. *A–C*, × 1; *D–F*, × 1½.

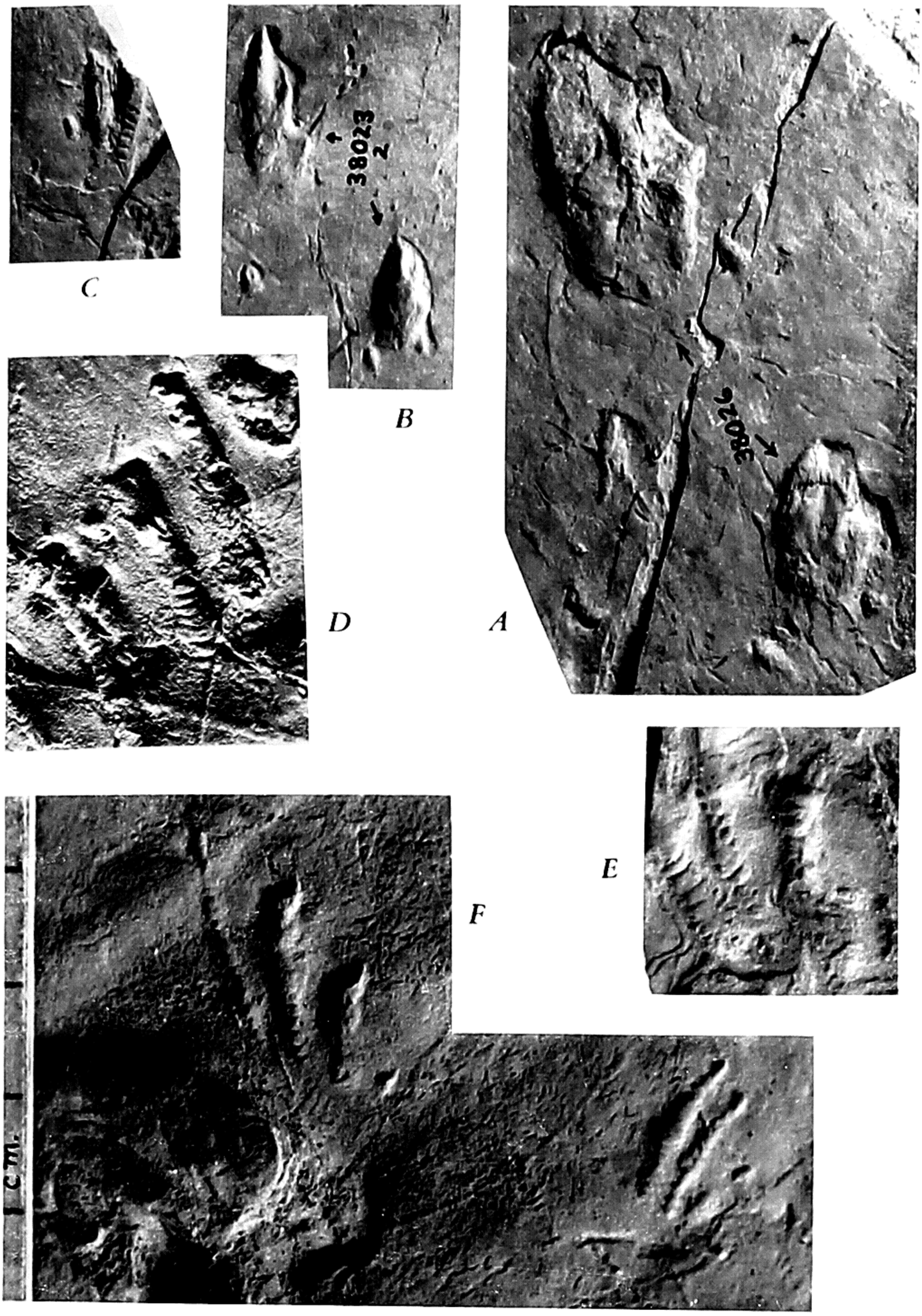

38023
2
38026
C
B
D
A
E
F
cm.

PLATE 33

Part of trackway surface enclosed by rectangle no. 1 in fig. 21, showing trackways of *Chirotherium diabloensis:* type, no. 36819; running trackway with associated tail mark, no. 36820; smallest trackway, no. 36823. × ½.

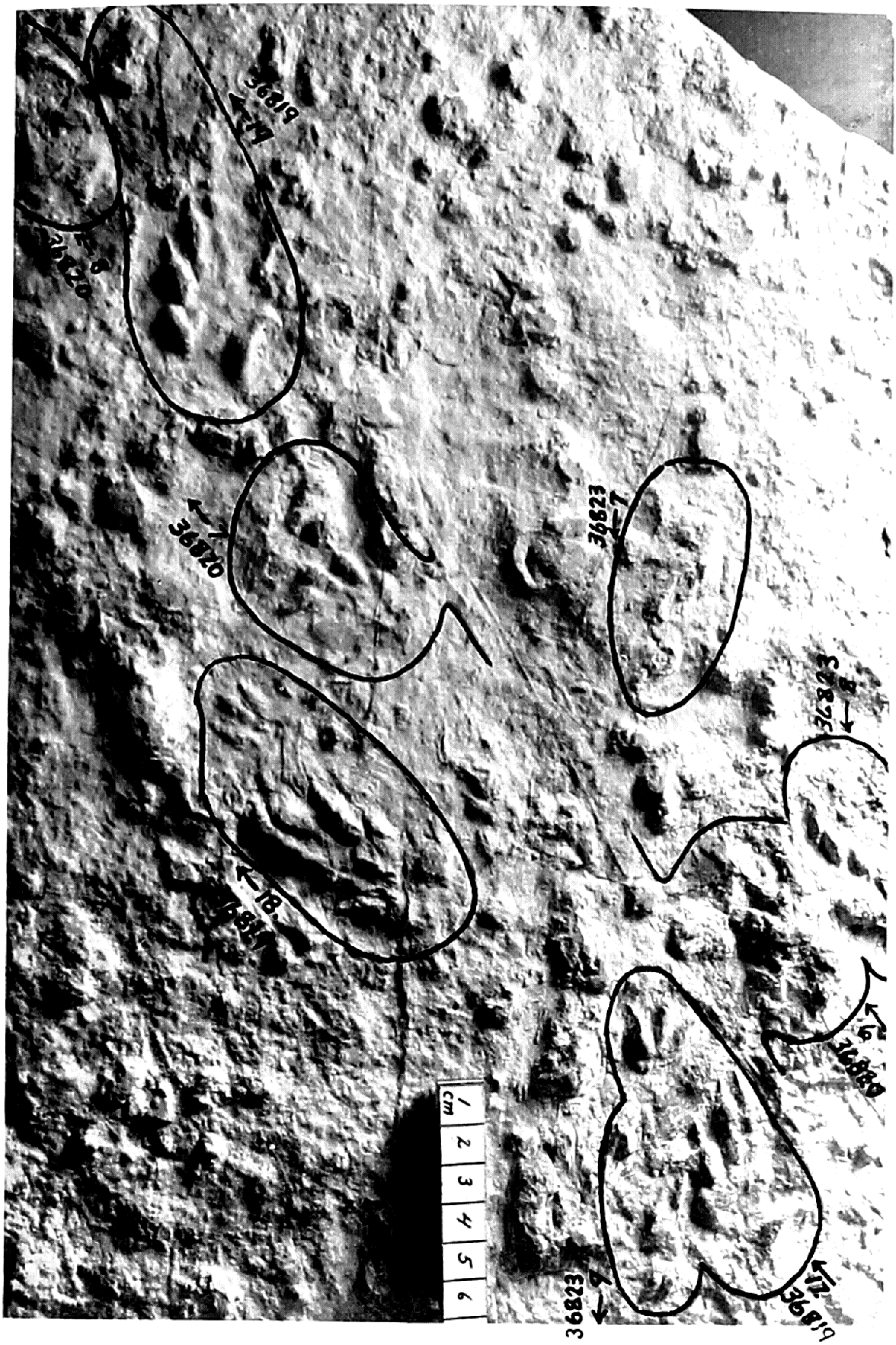


PLATE 34

Part of trackway surface enclosed by rectangle no. 2 in fig. 21, showing trackways of *Chirotherium diabloensis:* type, no. 36819 (right) paralleled by running trackway of smaller individual, no. 36820 (left). Note widespread digits of the pes in running trackway. × ½.


36820
36819

PLATE 35

Pl. 35, *A* and *B*, part of trackway surface enclosed by rectangles nos. 3 and 4 in fig. 21, showing trackway of *Chirotherium diabloensis* paratype, no. 36822. Tail mark shows between steps in "A." Note tail mark of *Rotodactylus* crossing step 1 of *Chirotherium* in "A." *C*, isolated set of manus and pes impressions of *C. diabloensis* showing associated tail mark, articular bulges on the manus digits, and metatarsal ridges on the pes. *A* and *B*, × ⅔; *C*, × 1.

A

C

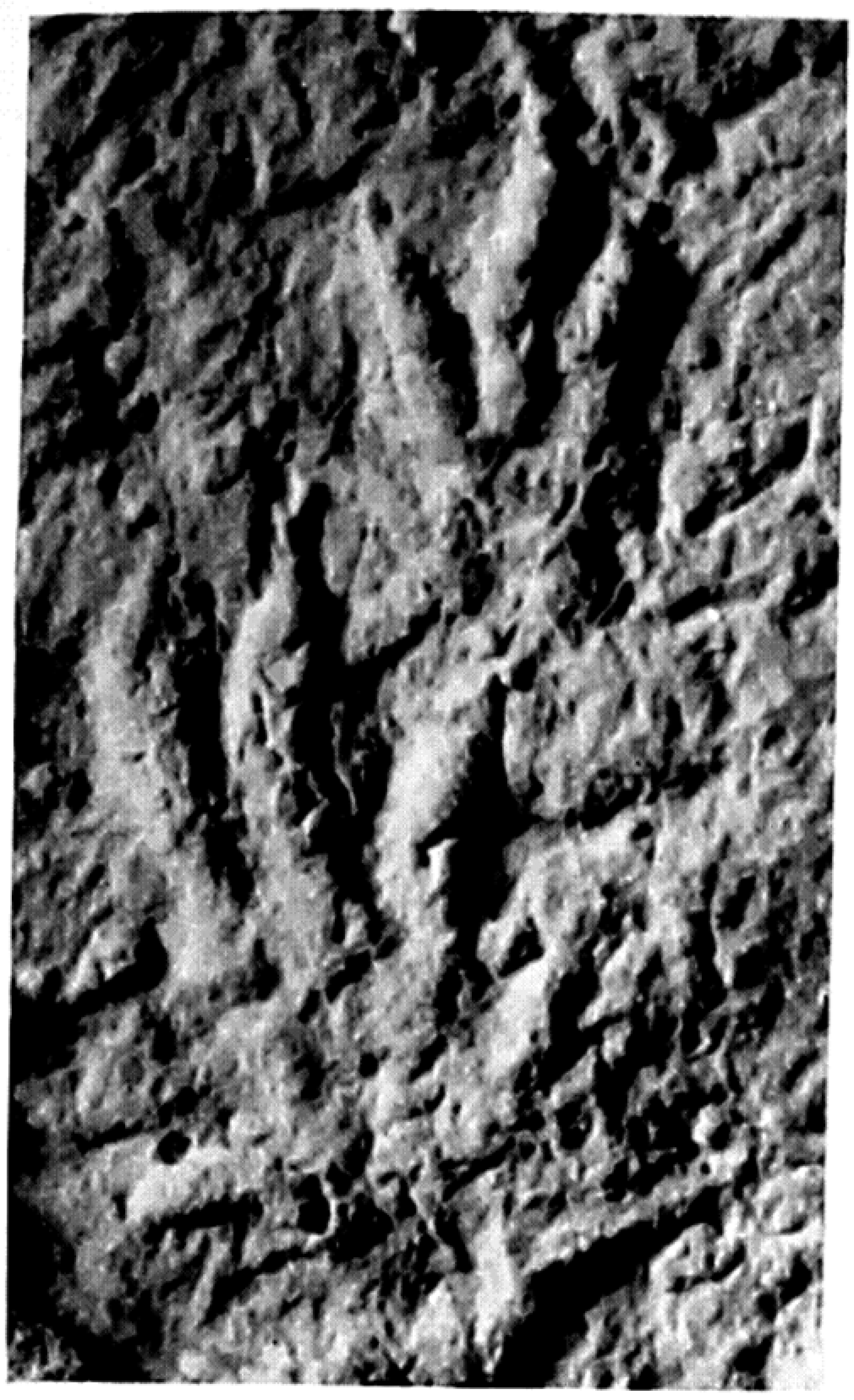
B

PLATE 36

Chirotherium cameronensis (type): *A*, manus and pes from trackway of four consecutive steps; *B*, manus and pes based on composite detail of trackway. × 1.

Lower figures show reconstructions of *Chirotherium barthi* body form, (upper) as depicted by Lyell in 1855, (lower) as depicted by Soergel.

A



B

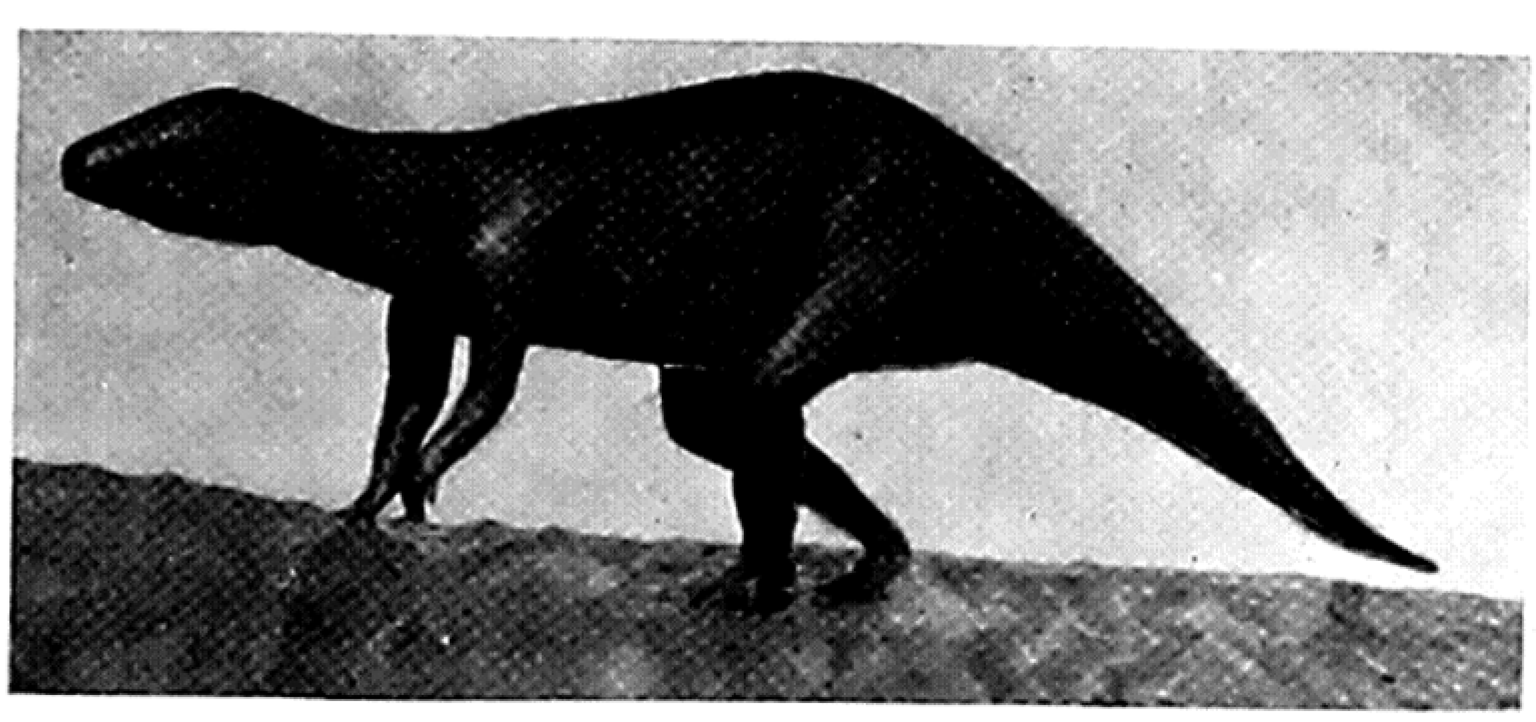


PLATE 37

Chirotherium minus; trackway of seven consecutive steps cast from a desiccated mudflat surface occurring in the Lower Moenkopi, Meteor Crater loc. map at "*a*." Area of photograph indicated by rectangle in fig. 16. Note missing pes digit V in steps 2, 3, and 6. $\times \frac{1}{6}$.

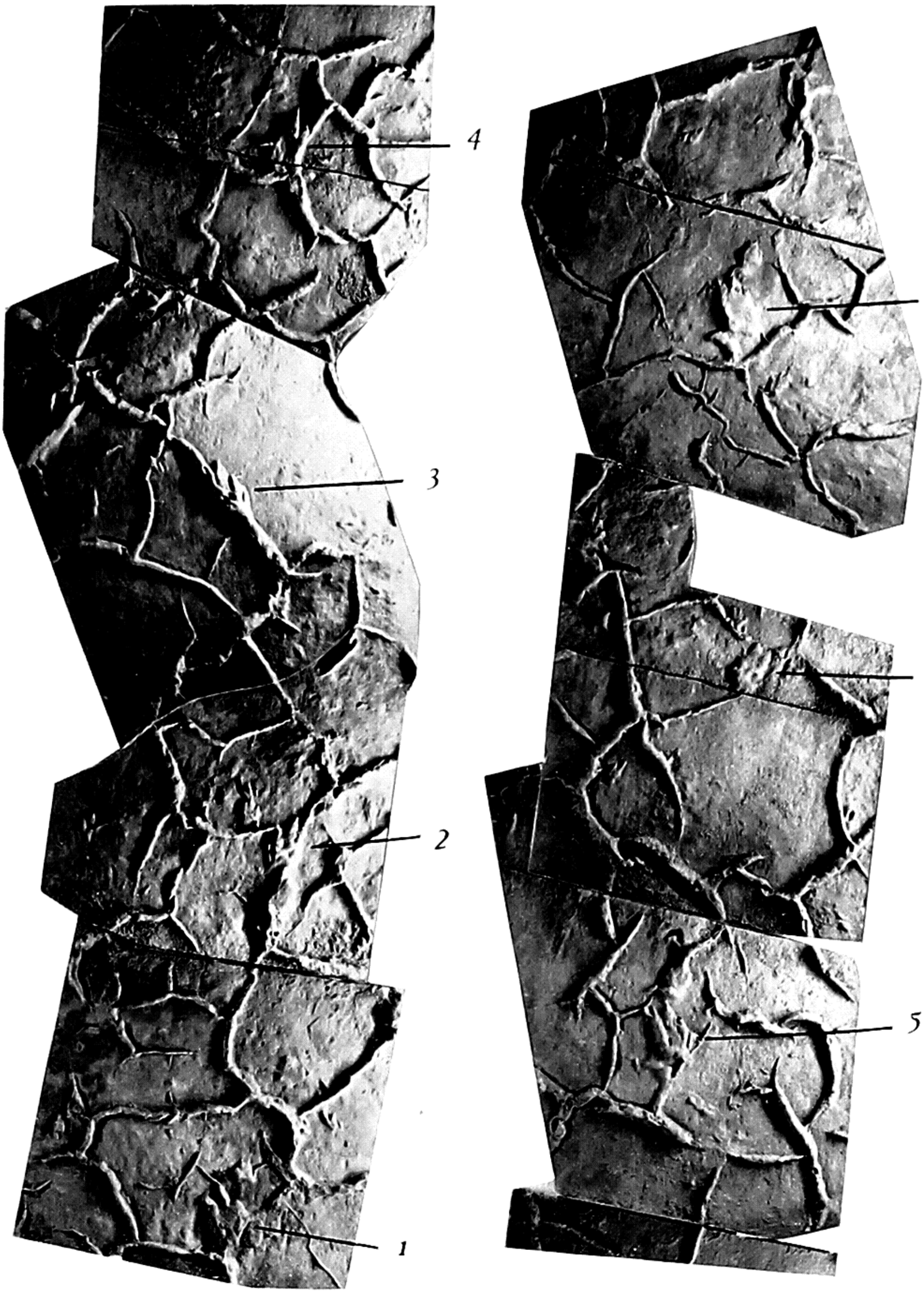

4
3
2
1
7
6
5

PLATE 38

Chirotherium minus; isolated footprints showing variability of impression: *A* and *B*, different positions and contours of manus digit V; *A*, *C*, *D*, *E*, details of pes digit V and characteristic knobby contours of pes digit IV; *E*, pes digit IV giving clear indication of five phalanges. × ⅔.

C

A

B

E

D

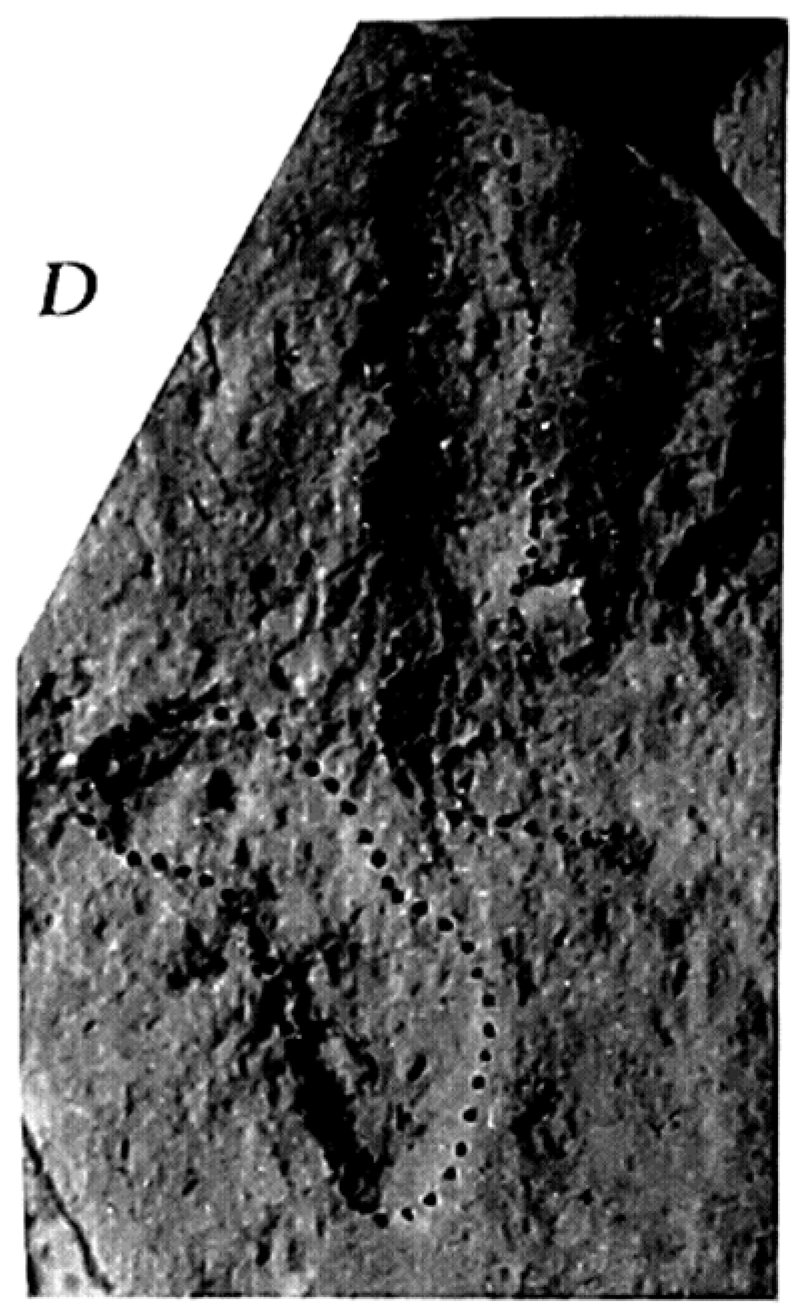


PLATE 39

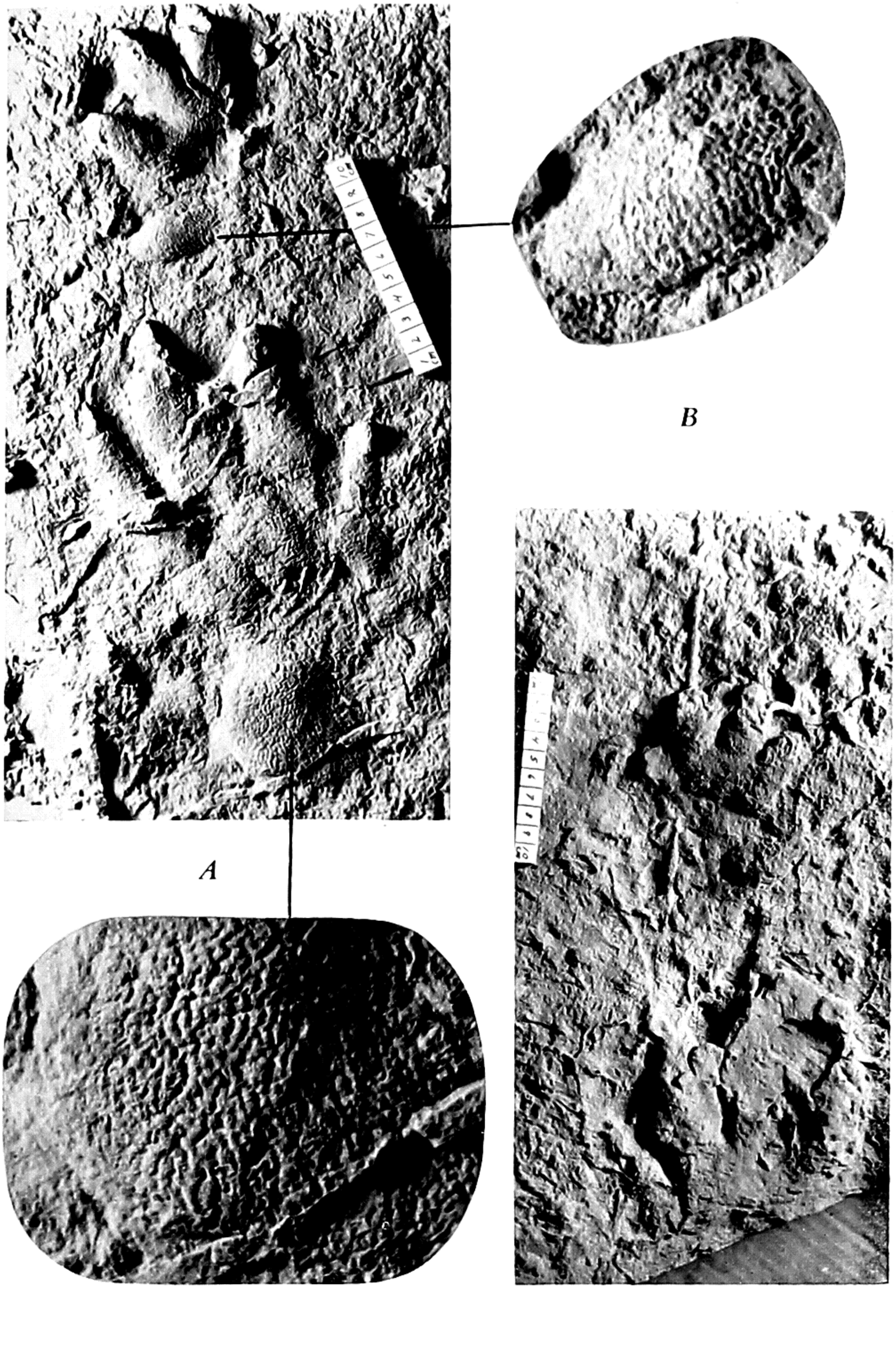
A, *Chirotherium barthi* from Upper Moenkopi near Cameron. Note pes of small individual on left edge of slab. Mus. Northern Arizona no. G2.2612 (photograph by L. F. Brady). *B*, trackway of small individual showing the relatively slender pes digit V. Note set of footprints of large individual at lower left edge of slab. M. N. A. no. G2.2127.

A

B

PLATE 40

A, ***Chirotherium barthi;*** **isolated set of footprints showing excellent detail, particularly of the scaly plantar surface. Enlarged areas (× 1) are of manus and pes digit V.** ***B,*** **set of footprints with associated tail mark.**



A

B

PLATE 41

A, pes of giant chirotheriid from upper Moenkopi of Rockville, Utah, loc. V4603, apparently similar in important respects to *Chirotherium moquiensis*. Areas of the plantar surface are enlarged (× 1) to show detail of the scales. *B*, lateral view of the pes showing where fringe scales left nearly vertical furrows on the lateral side of digit V and IV.

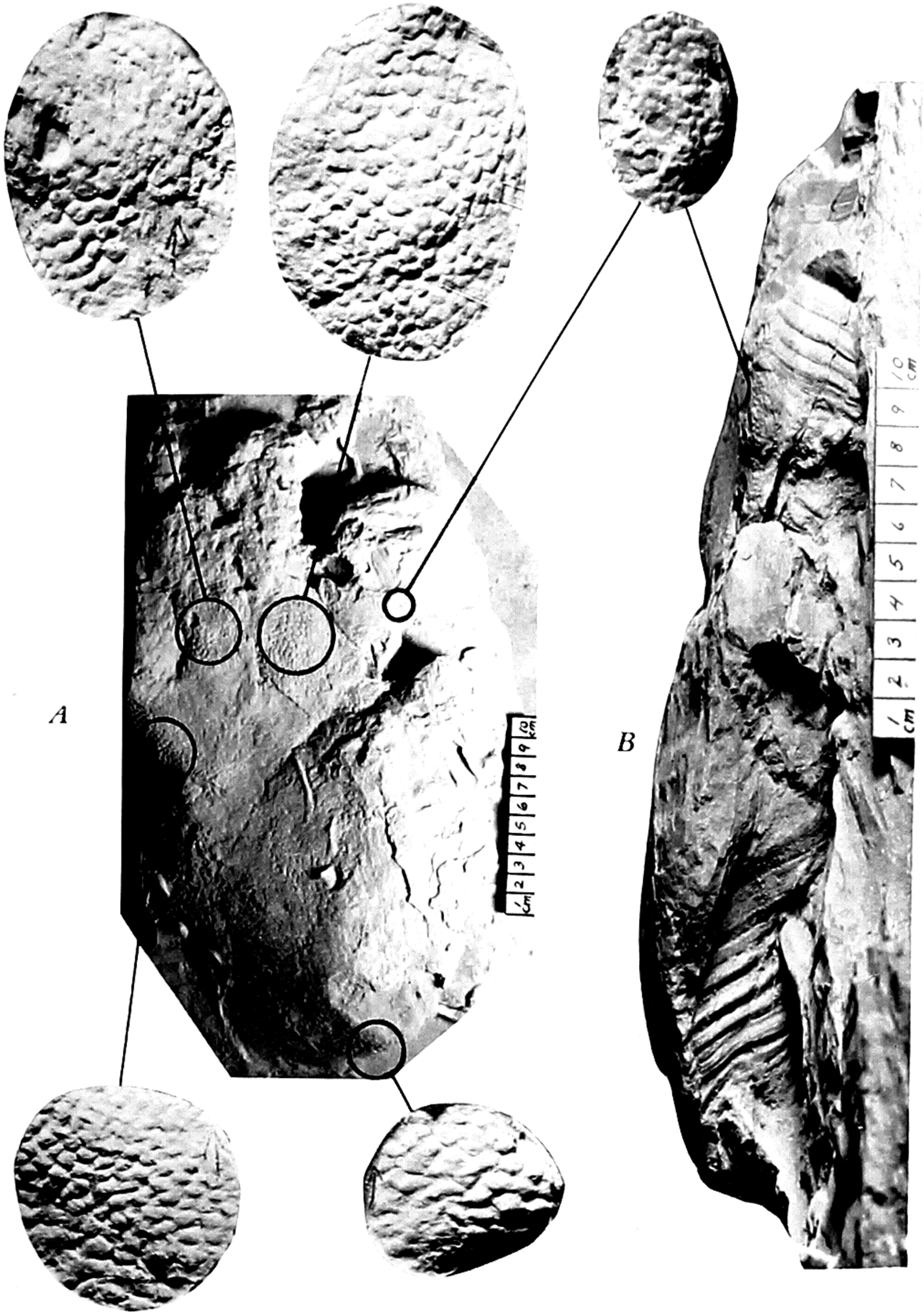
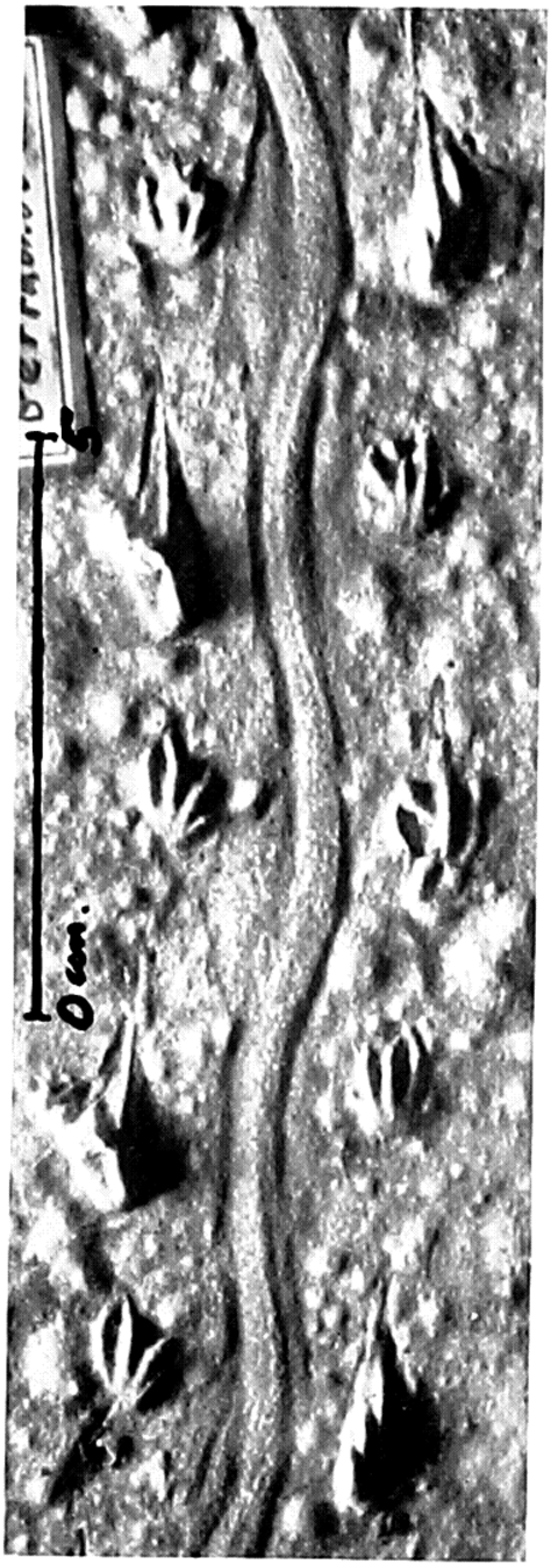

A
B
1 cm
2
3
4
5
6
7
8
9
10 cm

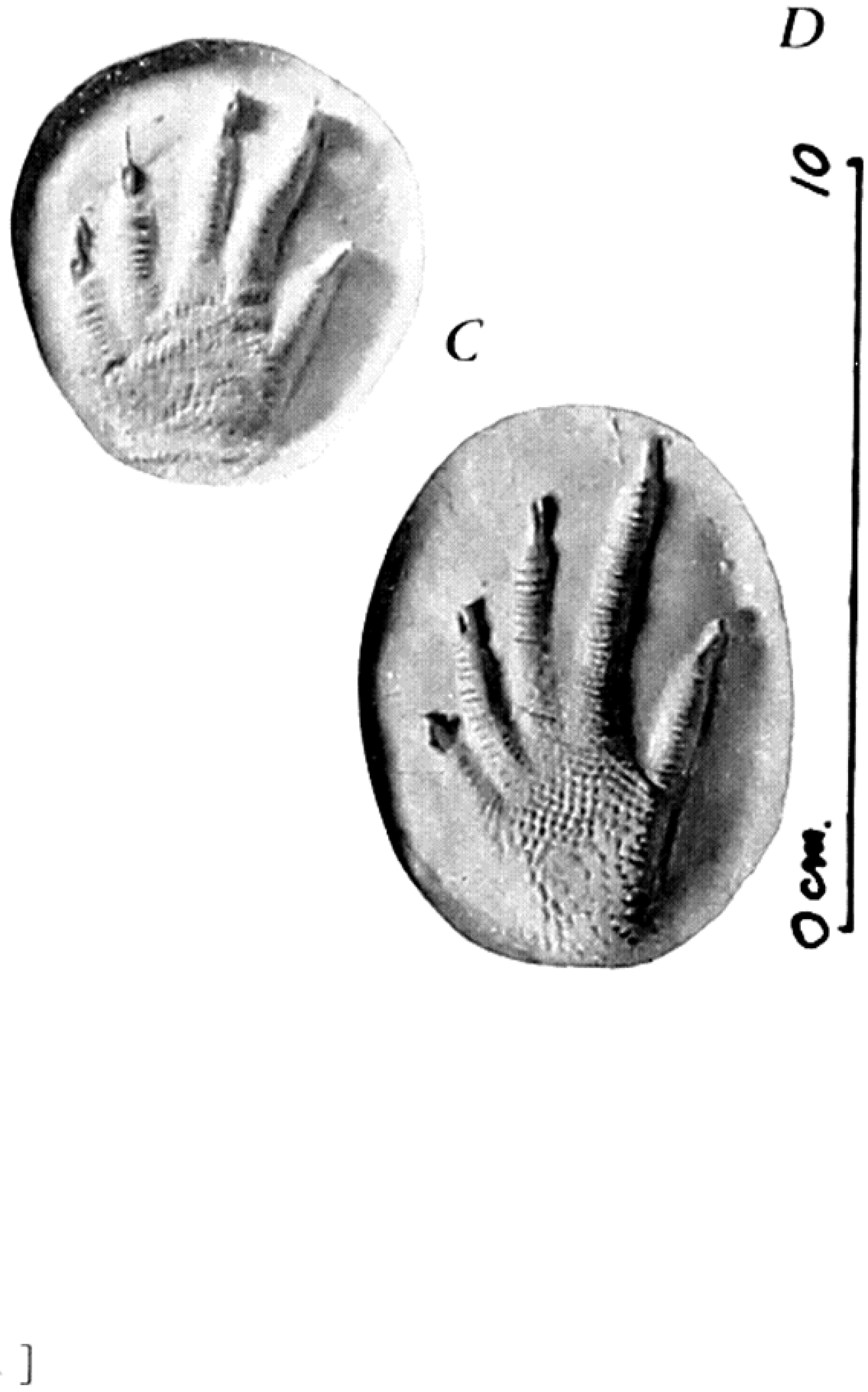
PLATE 42

A, trackway (cast) of a long-bodied lizard, *Gerrhonotus coeruleus*, found on a recent mudflat. *B*, manus and pes impressions from the trackway of a short-bodied lizard, *Sceloporus occidentalis*, also from a recent mudflat. *C*, manus and pes impression taken from pickled specimen of sphenodon, Calif. Acad. Sci. no. 47990. *D*, pes of *Chirotherium moquiensis* type, from the Lower Moenkopi of Moqui Wash, loc. V4126.



A

D



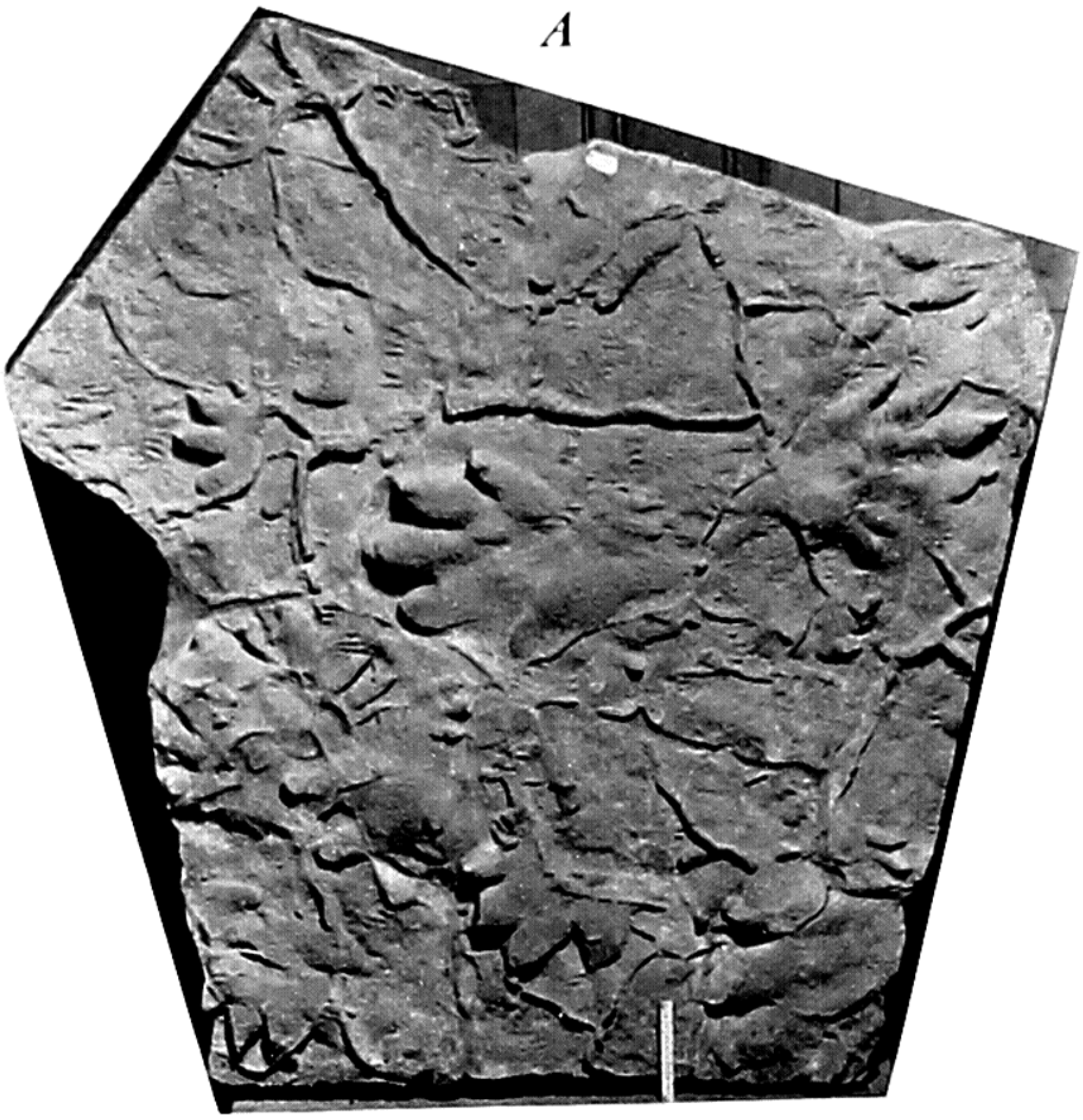
C

B

PLATE 43

A, trackway surface from Upper Moenkopi south of Cameron, showing the giant chirotheriid, *Chirotherium rex*, associated with *C. barthi*. Trackway surface is part of that shown in pl. 25, *A*. *B*, diagram of slab showing clearly how *C. rex* (stippled) dwarfs a very large specimen of *C. barthi*.

A



B

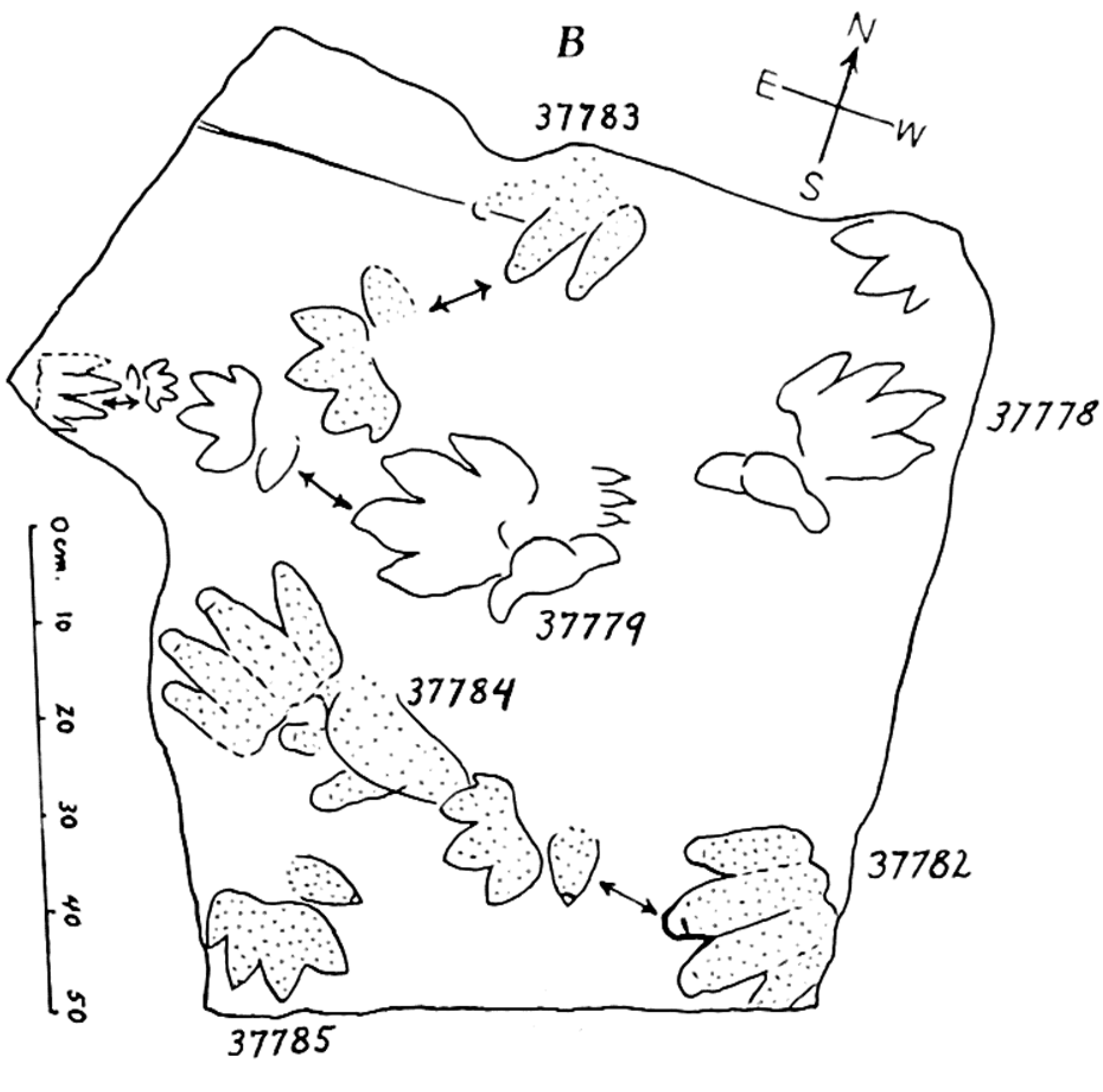


PLATE 44

A, *Chirotherium coltoni* (type) ; isolated set of footprints from the Lower Moenkopi, Meteor Crater loc. map at "*b*." *B* and *C*, *Chirotherium marshalli* (type) ; manus and pes impressions from trackway surface shown in fig. 31, *A*. See fig. 30 for line drawings.

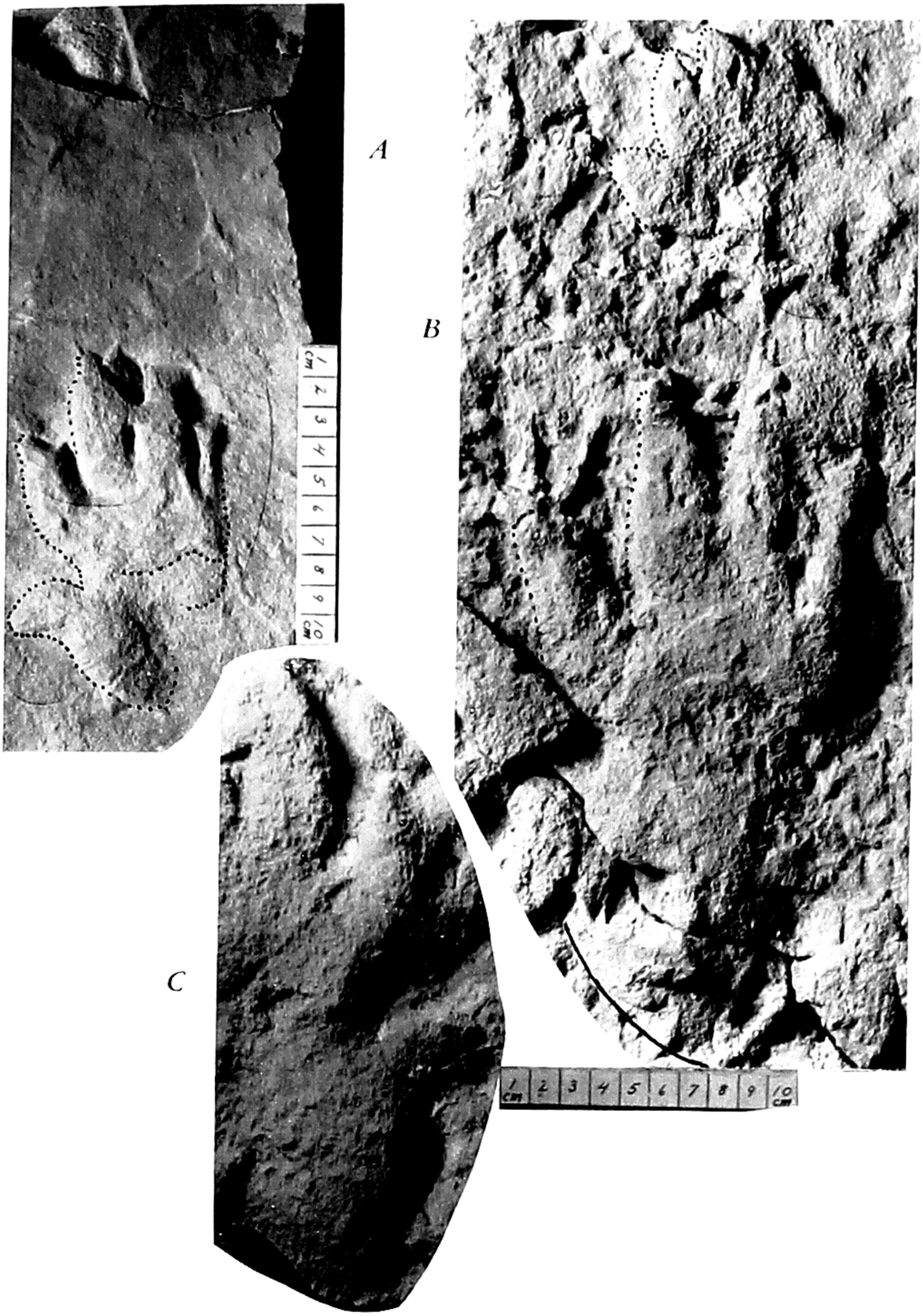

A
B
C
1 cm
2
3
4
5
6
7
8
9
10 cm
1 cm
2
3
4
5
6
7
8
9
10 cm

PLATE 45

Chirotherium sp. which is apparently bipedal, from the Lower Moenkopi of Moqui Wash. Note crescentic "current indicators" on upper left area of slab, and numerous lacertoid footprints. Slightly oblique view; tape measure is in inches.